THE ENVIRONMENTAL IMPACT OF ANTHROPOCENTRICALLY INDUCED PREDICTABILITY

LIVIA GOODBRAND

The environmental impact of anthropocentrically induced predictability

By

© Livia Goodbrand

A thesis submitted to the
School of Graduate Studies
In partial fulfilment of the
requirements of the degree of
Master of Science
Department of Biology
Memorial University of Newfoundland
September 2012
St John's, Newfoundland

Abstract

Variability is inherently an important characteristic of natural ecosystems. Like any other parameter that may define an organisms' environment, selection has favoured traits and strategies that exploit patterns in the variability of fluctuating physical and biological resources. Here I consider the ways in which animals may be affected by anthropogenic change that reduces variability in natural ecosystems.

Through many anthropogenic activities, we have inadvertently introduced resource patches into the environment that are fixed in space and that provide animals with regular access to food through time. These predictable food patches have become ubiquitous, and represent a fundamental change for animals that have adapted to a relationship between variability and scale. I provide a theoretical framework through which we can begin to understand the consequences of breaking such a relationship for animals that use information to make foraging decisions. I conclude that predictable resource patches should be favoured by foraging animals because the energetic costs of obtaining information are reduced at these sites.

I use the ideal free distribution (IFD) theory to test the hypothesis that animals will prefer to forage where resource distributions have become predictable. Given the choice between patches of equal value but that differed in the temporal predictability of their food, juvenile cod gradually developed a preference for the predictable patch over a 5-day experimental period. This preference occurred simultaneously with a reduction in patch sampling behaviour, suggesting that cod were able to reduce the costs of obtaining information at the predictable patch.

Having observed that the distribution of cod shifted towards the predictable patch in an experimental setting, I examine the effects of introducing a predictable resource patch into a natural environment. Aquaculture sea cages are fixed in space and inadvertently provide stable access to resources to wild animals through time. I consider the effect of sea cages on the distribution of wild fish in coastal marine environments, in which patterns of fluctuating resources are distinguished by a large magnitude of variability. I demonstrate that sea cages can alter the distribution of marine life at large spatial scales, suggesting that there is an energetic advantage to foraging at these sites. Understanding the costs and benefits of this behaviour is needed to predict the outcome of anthropogenic changes that alter patterns of variability in natural ecosystems.

Acknowledgements

At the end of each chapter, I have acknowledged those individuals who made significant contributions specific to that work. Here, I happily take the opportunity to thank those who supported my endeavors on a more personal note, and to recognize those whose support was essential to the realization of this degree.

First and foremost, I thank M. Abrahams for his unending patience and support. For better or for worse, he allowed me to pursue all of my scientific whims. I can only hope that I leave this place having assumed some of his diplomacy and calmness of thought.

I am indebted to G. Rose for giving me the opportunity to develop my sea legs and for teaching me about cod. There is nowhere else on Earth that I could have had these experiences.

I thank Mom and Amanda for listening to me complain about the weather and for helping me see through challenging times. Finally, I thank Corey, my partner, for his unconditional friendship, his stability, and for keeping our dream afloat.

Contents

List of Tables

List of Figures

List of Appendices

Chapter 1. General introduction

Understanding the direction and magnitude of anthropogenic environmental change has become a unifying pursuit amongst ecologists worldwide. Though ecologists from diverse backgrounds may aspire to solving the same problem, “what is the effect of human activity X on the environment”, communication between different fields in ecology has often been limited. The result has been patchy assemblages of studies that address context-specific problems.

This lack of communication is not limited to applied fields in ecology. In my own literature search, I found several examples of interconnecting areas of theoretical research that exist in isolation because of semantic differences. For example, theories of risk sensitivity could be naturally synthesized with broader models of habitat choice, if not for the use of ‘risk’ in place of ‘variability’. Similarly, the investigation of resource pulses and prey hotspots address an analogous question, “how do animals respond to resources that are spatially and temporally auto correlated”, but this question is asked for animals occupying different trophic levels. After observing several examples of how literature in the ecological sciences was being compartmentalized, and consequently ignored by other fields in ecology, I proposed to create a thesis that could provide a conceptual framework for my own-and future- studies, while synthesizing several fields in ecology that had not yet engaged in conversation. To that end, ‘The Environmental Impact of Predictability’ provides the reader with a comprehensive overview for the study of resource predictability.

The central and unifying concept that I address in my thesis is that animals are adapted to natural patterns of environmental variability that are scale dependent. Drawing from the long history of discussion on the 'problem of scale' in ecology (Wiens 1989; Steele 1991), I resurrect Levin's (1992) fundamental observation, that variability is a function of the size of the window through which one views the world; as we increase the size of our window, variability tends to decay. From an animal's perspective, this simple relationship governs the world it lives in. What then are the consequences of changing this relationship? I argue that many human activities have inadvertently broken this relationship, through the introduction of highly predictable resource patches. In doing so, we have changed the way animals experience and interact with natural patterns of environmental variability to which they have adapted.

To address the environmental impact of predictability, I use a combination of theoretical, experimental, and field approaches. Chapter 2 of this thesis introduces the concept of environmental predictability using examples from the foraging literature. A theoretical framework is then developed for understanding the effects of environmental change that act to reduce variability on animals that use information to make foraging decisions. I develop the hypothesis that animals should prefer to forage where resource distributions have become predictable because they can save on the energetic costs of obtaining information. Chapter 3 presents experimental support for this hypothesis. Finally, Chapter 4 looks for the effects of predictability on animal distributions in the field, using aquaculture sea cages as an example of predictable resource patches that have been introduced into an otherwise stochastic environment.

References

Levin, S. (1992). The problem of pattern and scale in ecology. *Ecology*, 73, 1943-1967.

Steele, J. (1991). Can ecological theory cross the land sea boundary? *J.Theor.Biol.*, 153, 425-436.

Wiens, J. (1989). Spatial scaling in ecology. *Funct.Ecol.*, 3, 385-397.

Chapter 2. The environmental impact of predictability

Livia Goodbrand[1*] and Mark V. Abrahams[1]

*[1] L. Goodbrand (Livia.Goodbrand@mun.ca), Department of Biology, Memorial University of Newfoundland, St. John's, NL, Canada A1C 5S7, Phone: (709)864-7493, Fax: (709)864-3316

[1]M.V. Abrahams (Mabrahams@mun.ca), Department of Biology, Memorial University of Newfoundland, St. John's, NL

The environmental impact of predictability to be submitted as a *Concepts and Synthesis* article

Abstract

For ecologists, variability is an inherent property of the organisms and systems we seek to understand. Confounding issues of variability in ecological data is the dependence of variability on spatial and temporal scale; for example, what appears to be random or stochastic at small scales of observation may appear predictable when viewed through a larger lens. If patterns of variability are inherently dependent on scale, it is reasonable to suspect that selection has worked on behavioural traits and life history strategies to exploit this relationship. Using examples from the foraging literature, I present a novel perspective on how the information strategies used by animals are adapted to the natural relationship between environmental predictability and scale. Changing this relationship through anthropogenic activities may have consequences for organisms that are adapted to cope with or exploit natural patterns of environmental predictability. I suggest that the study of resource predictability is important because the introduction of novel and highly predictable resource patches is wide spread, and may have an ecosystem effect.

Keywords: information; predictability; variability; scale; environmental impact; habitat quality

Introduction

A hallmark of ecology is variability. While this is often the bane of existence to those that study ecology, it is the environment that our study systems and organisms are adapted to. Variability is not an absolute, however, and its description depends on the spatial or temporal scale at which it is being observed. Its effect on the behaviours and life histories of organisms must therefore be discussed with reference to the scale of that organism's environment; for each organism will realize environmental variability as a consequence of the scales of its own experience (Levin 1992). For animals that experience their environment through a microscopic lens, the world is an unpredictable place, governed by stochastic processes and phenomena. At increasingly large spatial and temporal scales, stochasticity gives way to pattern in the variability of fluctuating physical and biological resources, which can become predictable when viewed through a macroscopic lens (Weins 1989; Levin 1992). In this chapter, I use examples from the foraging literature to explore the ecological importance of variability, the acquisition and use of information for surviving in a variable environment, predictability and its ecological scale, and predictability as an anthropogenic effect.

The Ecological Importance of Variability

One of the most important tools for ecologists is statistics. Many other disciplines use statistics, but depending upon the parameters being measured, ecology is often distinguished by the magnitude of the variation within data collected from natural systems. In part, this is driven by the large number of parameters that can act simultaneously on the parameter of interest. The combination of these parameters may result in complex data sets that require sophisticated analyses to distinguish patterns from noise. While that may be the reality of the ecologist trying to understand such a system, the reality of organisms that have evolved within these systems is that variability is a part of their world. Like any other parameter that may define their environment, selection has favoured traits and strategies that exploit patterns in the variability of fluctuating physical and biological resources (e.g. Levin 1992 and references therein). Though variability is intuitively an important characteristic of any ecosystem, a fundamental question in ecology is why? A simple answer may be that it is important not to be too predictable. Ecosystems define mechanisms by which energy flows from one trophic level to another, yet they are filled with participants that are trying to thwart this process; nobody wants themselves or their kin to be somebody else's lunch. One tactic for survival therefore is to make it difficult for your predators to locate you in time and space. For predators, the challenge is to filter useful information on the distribution of its prey from environmental noise.

Obtaining information in a variable environment

Whether deciding where to forage, how to avoid predators, or with whom to mate with, all animals use their senses to obtain information for decision making in variable environments. For animals with multiple sensory systems, what senses should be used to obtain information depends on two factors: the physical characteristics of its environment and the characteristics of its desired resource. This is illustrated by observations of the generalist predatory fish *Pseudophycas barbata*, which employs multiple non-visual sensory systems to nocturnally hunt for prey items (Bassett and Montgomery 2011). Both its chemo- and mechano-sensory systems are adaptations for locating prey in low-light conditions, and can be used simultaneously to find a diversity of prey items at night. It is the prey's behaviour that determines the relative efficacy of either sense; *P. Barbata*'s lateral line is best at detecting mobile prey items that emit a hydrodynamic signal, while its chemosensory barbells are best at detecting still-lying or sessile prey items. Similarly, for the detection of predators, Hartman and Abrahams (2000) show that fathead minnows (*Pimephales promelas*) can respond to both chemical or visual alarm cues, and its response to one or the other will depend on the combined effects of its environmental conditions (turbidity) and its perceived risk of predation. The information that an animal obtains from one or more of its senses can be best understood as a commodity or resource that enhances its fitness by affecting behavioural change (Stephens 1989; Dall *et al.* 2005). Like any resource, the acquisition of information comes at an ecological price.

Evidence for the cost of obtaining information primarily comes from the foraging literature. The costs of obtaining information for foraging decisions include direct costs, such as the time and energy spent searching for information via patch sampling, as well as missed opportunity costs: time spent collecting information on the distribution of resources may be time away from consuming food items (Eliassen *et al.* 2007; 2009). A considerable amount of energy is also spent on maintaining the sensory and neural capacity for obtaining and processing information, respectively (reviewed in Niven and Laughlin 2008). These costs relate to the acquisition of information through your interactions with your environment, which is known as personal information (Valone 1989).

The costs of obtaining information can be reduced if you rely on information that has been collected by others, or public information (for review, see Danchin *et al.* 2004). For example, information exchanged between individuals in breeding bird colonies (the information center hypothesis; Ward and Zahavi 1973) is thought to increase individual fitness by reducing search costs for resource patches that are characteristically patchy and unpredictable through space and time (for a more recent review, see Barta and Giraldeau 2001). While public information reduces the individual costs of obtaining information, the potential benefits of that information also decline because it is less reliable and is shared between multiple individuals (Templeton and Giraldeau 1996); thus if personal information can be obtained easily and at a low cost, public information should be ignored (Valone and Templeton 2002).

Other forms of information are available to social animals as well. For example, by mimicking the behaviour of others, an individual can learn about how, when, and where to find food resources (social foraging reviewed in Galef and Giraldeau 2001). Of course, there are costs and benefits to using social information as well (reviewed in Rieucau and Giraldeau 2011). In many cases, our understanding of the types of information that are available to animals and how this information is shared between individuals is incomplete (Galef and Giraldeau 2001).

The use of information for surviving in a variable environment

Obtaining information through private interactions with the environment, or through interactions with other individuals, can help an animal survive in variable environments. But what do you do with the information that you have acquired and when do you use it? If there are costs associated with acquiring and using information, how much should you be willing to pay for it?

Attempts to answer questions that relate to the use of information as a fitness enhancing resource are currently being addressed within foraging theory, but the importance of information is not limited to its utility for acquiring food resources. Information is also used to cope with variability in the risk of predation (predation risk allocation hypothesis, Lima and Bednekoff 1999; Ferrari *et al.* 2008), in signal reliability (McLinn and Stephens 2006), and in mate choice (reviewed in Jennions and Petrie 1997). Since variability is an inherent property of natural ecosystems, the use of information pertains to all biologically important aspects of an animal's life history.

In the foraging literature, there are two strategies that describe an animal capable of using information to increase its success in a variable environment. The Bayesian forager can estimate patch quality by comparing information on current patch quality to knowledge it has obtained on the distribution of resources among food patches through sampling. The prescient forager can make accurate and immediate assessments of current patch quality and remember its estimate of patch quality for future foraging decisions (Valone and Brown 1989). The 'smarter' prescient forager is able to forage more efficiently than the less informed Bayesian forager (Valone 1991, 1992; Vasquez *et al.* 2006), but it pays a heavy energetic price to maintain the sensory capacity necessary to do so (Olsson and Brown 2010). The alternative is to forage without information (e.g. fixed time foraging), and pay the 'penalty of ignorance' (Olsson and Brown 2006). Using information should therefore be considered a trade-off between the energetic costs and benefits of being informed in a variable environment. The benefits will be defined relative to the information states (Olsson and Brown 2010) and competitive abilities (Koops and Abrahams 2003) of your competitors.

In order for an information strategy to be adaptive, the fitness gains of investing in information must outweigh the sum of the energetic costs of obtaining it (Olsson and Brown 2010), regardless of its application. Selection can only favour adaptations for information use, however, if the information that is available to animals can reliably predict an outcome (e.g. food availability, predation risk, or mate quality) most of the time. In a truly stochastic environment, the probability that information collected today will be useful tomorrow is low, and consequently the value of investing in expensive environmental information is also low (Eliassen *et al.* 2009). Occupying a niche where patterns in natural variability have become predictable should be advantageous to animals that invest in information to increase their fitness, because there is some guarantee that prior information will reliably describe the current state of its environment. Predictability, after all, is a measure of reliability (index of predictability, Colwell 1974), and the value of information increases as its reliability increases (Koops 2004). In a truly unpredictable environment, if the information an animal has obtained cannot reliably predict quality, and energetic investments in energy do not pay off, then using information is maladaptive.

Predictability and its ecological scale

For ecologists, describing patterns of spatial or temporal variability is dependent on the scale of our observation. In general, variability decays as we increase the size of our window of observation (Levin 1992). As a result, ecological processes and patterns of fluctuating resources become increasingly predictable with increasingly large spatiotemporal scales (Fig. 2.1). The exact relationship between variability and scale is difficult to predict (see Levin 1992 for discussion), especially in heterogeneous environments. However, this pattern has been described theoretically (Wiens 1989; Levin 1992), and observed in natural systems using a variety of empirical measures (e.g. Costanza and Maxwell 1994; Fuhlendorf and Smeins 1996; Navarrete *et* *al.* 2008). When viewed through a macroscopic lens, the world becomes a predictable place, governed by physical forces such as seasonality, ocean circulation, and atmospheric forcing.

To maximize predictability, this observation suggests that animals specializing in the exploitation of predictable resource distributions should be adapted to forage across large spatial and temporal scales. Notable examples of animals that are adapted to forage at scales that maximize predictability include basking sharks (*Cetorhinus maximus*) that forage on seasonal zooplankton blooms (Sims *et al.* 2006); Atlantic cod (*Gadus morhua*) feeding on spawning capelin (*Mallotus villosus*) (Rose and Leggett, 1988); killer whales (*Orcinus orca*) feeding on migratory Pacific salmon (*Oncorhynchus spp)* (Nichol and Shackleton 1996); and many sea birds that forage on seasonally available prey fish (reviewed in Weimerskirch 2007). For these animals, a bad decision will likely be fatal or result in a failed reproductive season because the energetic investment they have made is so great. The life history strategies of animals that migrate across large spatiotemporal scales are adaptive, because at large scales, resource distributions are predictable and bad decisions are unlikely to occur.

Information strategies and scale

From an animal's perspective, the significant consequence of the relationship between environmental predictability and scale is that information used for the assessment of environmental quality becomes more reliable with increasing scale. Information is expensive, but when it is reliable, energetic investments in information pay off; for example, better informed animals have better foraging success (Valone 1991, 1992; Vasquez *et al.* 2006; Olsson and Brown 2006, 2010; Van Gils 2010). However, it is the balance between the costs and benefits that determine the adaptive value of information. The benefits of acquiring information can only outweigh the costs when information is reliable, enabling energetically expensive information strategies such as prescient foraging to be favoured amongst animals with large scales of experience.

For animals that can rely on prior information for the assessment of environmental quality, the acquisition of additional current information is redundant, provided the environment is unchanged from their prior assessment. Consider an example of an animal that has perfect information on the distribution of resources within its environment, which it can recall from memory of past foraging success. For this animal, no new information can be gained through sampling current patch quality, and energy spent on current patch assessment is superfluous. Since the acquisition of either current or prior information comes at an energetic cost, it is conceivable that there exists a trade off between the use of either strategy. Theoretically, the relative amount of energy invested in prior and current information will change in relation to the scale that an animal experiences its environment (Fig. 2), because of the positive relationship between environmental predictability and spatiotemporal scale. In the context of foraging theory, this means that information strategies that rely on prior information, such as prescient foraging, should be favoured amongst animals with large foraging scales that have access to reliable information; Bayesian foraging is a more economic strategy for animals that forage at small spatiotemporal scales.

Predictability as an anthropogenic effect

If animals are adapted to use information in an environment where predictability depends on spatial and temporal scale, what happens when the relationship between predictability and scale is broken (Fig. 3)? Through anthropogenic activities, we have inadvertently created novel habitats where the distribution of resources can be highly predictable, at small spatial and temporal scales. For example, backyard bird feeders, sewage outflows, aquaculture sea cage sites, garbage dumps, and agricultural fields provide food resources to wild animals that are predictably available through space and time. In doing so, we have fundamentally changed the utility of information for many foraging animals. What is the environmental impact of anthropogenic predictability?

From a cost/benefit perspective, bird feeders, sea cages, and other novel resource patches provide all of the advantages of environmental predictability, free of charge. Predators that specialize in the exploitation of predictable prey distributions can stay home and reliably obtain the resources they need without investing in long-range travel and expensive information strategies. Animals that could not previously afford to obtain reliable information can access the same information as 'smarter' individuals, populations, or species, at low energetic cost. Hence there may be a net benefit to foraging at these predictable resource patches. But can this 'infocentric' foraging be truly cost free?

I suggest that the introduction of predictability into natural ecosystems has been widespread and its effect on consumer responses should be considered at the individual, population, and community level. From a scattering of studies, we know that the introduction of novel food sources can affect the natural histories of animals, across different ecosystems. For example, the large scale diet supplementation of avian populations by backyard bird feeders has resulted in population increases and range expansions for many northern migratory species (reviewed in Robb *et al.* 2008). In a similar way, dense, multi-species aggregations of wild fish are attracted to aquaculture sea cages (Sanchez-Jerez *et al.* 2011), where the consumption of excess pellet feed can improve their body condition relative to non-cage associated wild fish (Fernandez-Jover *et al.* 2007; Dempster *et al.* 2011). In the past, we have considered these effects in the context of nutrient additions into the environment. What has not been considered is that the sum of these artificial feeders is the creation of novel ecosystems in which the spatial and temporal distribution of food resources is highly predictable through space and time. This is a fundamental change for animals that are adapted to use information for survival in an environment where natural patterns of variability depend on scale.

Conclusions and perspectives for future research

The investigation of variability has forced ecologists to acknowledge 'the problem of scale in ecology' (Wiens1989; Steele 1991; Levin 1992; Schneider 2001). Rather than a nuisance, we now treat variance as a biologically important quantity that changes depending on the scale of our observation (reviewed in Horne and Schneider 1995). For animals, the statistical complexities of dealing with variance are irrelevant; variability is a natural part of the environment to which they have adapted, through both the exploitation of large scale predictability and through the selection for traits that can cope with small scale variability.

Our challenge is to consider the ways in which these adaptations will respond to changes in the relationship between environmental variability and scale. Having modified the spatial and temporal distribution of resource availability in many land- and seascapes, we must ask ourselves what the ecosystem effect of environmental predictability is. Does the sum of these novel resource introductions amount to a change in the way animal's interact with and perceive variability? Have we reduced variability in the periodicities of natural resource fluctuations, and in doing so, changed the adaptive value information? How can we measure this effect?

Experiments that manipulate the spatial and temporal predictability of resource distributions will be useful for estimating the net value of environmental predictability and information reliability. An energetic determination of the value of predictability will support field investigations at sites where resource distributions have become predictable, either naturally (e.g. upwelling regions) or through anthropogenic activity (e.g. aquaculture sea cages). If there is a net benefit to exploiting predictability, we would expect the abundance and distribution of animals to reflect this benefit. Among the individuals and populations that exploit predictability, can we define some patterns of physiological and behavioural responses to resource distributions that have become spatially and temporally predictable? How and whether individual and population-level effects are propagated across multiple trophic levels is a more challenging question to address and will require an understanding of the top-down and bottom-up effects of introducing predictability into an ecosystem. I believe that the introduction of predictable resource distributions is widespread and warrants investigation at the ecosystem-level. Since variability, information, and issues of scale are fundamental concepts in ecology, I suggest that the study of environmental predictability offers an opportunity to synthesize a number of exciting and emerging topics for ecologists.

Acknowledgements

My thoughts on this subject benefitted from conversations with D. Schneider, I. Fleming, J. Mitchell, D. Bassett and other colleagues at Memorial University. Financial support was provided by a Memorial University Graduate Fellowship to L. Goodbrand, and by NSERC, Memorial University, and Newfoundland Research Development Corporation Grants to M. Abrahams.

Literature Cited

Barta, Z. & Giraldeau, L. (2001). Breeding colonies as information centers: A reappraisal of information-based hypotheses using the producer-scrounger game. *Behav.Ecol.*, 12, 121-127.

Bassett, D. K. & Montgomery, J. C. (2011). The feeding response of *Pseudophycas barbata* to multisensory prey cues in a low light environment. *J.Fish Biol.*, 79, 526-532.

Colwell, R. (1974). Predictability, constancy, and contingency of periodic phenomena. *Ecology*, 55, 1148-1153.

Costanza, R. & Maxwell, T. (1994). Resolution and predictability - an approach to the scaling problem. *Landscape Ecol.*, 9, 47-57.

Dall, S., Giraldeau, L., Olsson, O., McNamara, J. & Stephens, D. (2005). Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.*, 20, 187-193

Danchin, E., Giraldeau, L., Valone, T. & Wagner, R. (2004). Public information: From nosy neighbours to cultural evolution. *Science*, 305, 487-491.

Dempster, T., Sanchez-Jerez, P., Fernandez-Jover, D., Bayle-Sempere, J., Nilsen, R., Bjorn, P. & Uglem, I. (2011). Proxy measures of fitness suggest coastal fish farms can act as population sources and not ecological traps for wild gadoid fish, *PLos One,* 6, 1

Eliassen, S., Jorgensen, C., Mangel, M. & Giske, J. (2007). Exploration or exploitation: Life expectancy changes the value of learning in foraging strategies. *Oikos*, 116, 513-523.

Eliassen, S., Jorgensen, C., Mangel, M. & Giske, J. (2009). Quantifying the adaptive value of learning in foraging behaviour. *Am. Nat.*, 174, 478-489

Fernandez-Jover, D., Lopez Jimenez, J. A., Sanchez-Jerez, P., Bayle-Sempere, J., Casalduero, F. G., Martinez Lopez, F. J. & Dempster, T. (2007). Changes in body condition and fatty acid composition of wild mediterranean horse mackerel (*trachurus mediterraneus, steindachner, 1868*) associated to sea cage fish farms. *Mar.Environ.Res.*, 63, 1-18.

Ferrari, M. C. O., Rive, A. C., MacNaughton, C. J., Brown, G. E. & Chivers, D. P. (2008). Fixed vs. random temporal predictability of predation risk: An extension of the risk allocation hypothesis. *Ethology*, 114, 238-244.

Fuhlendorf, S. & Smeins, F. (1996). Spatial scale influence on longterm temporal patterns of a semi-arid grassland. *Landscape Ecol.*, 11, 107-113.

Galef, B. & Giraldeau, L. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Anim.Behav.*, 61, 3-15.

Hartman, E. & Abrahams, M. (2000). Sensory compensation and the detection of predators: The interaction between chemical and visual information. *Philos. Trans. R. Soc. Lond. Ser. B* 267, 571-575.

Horne, J. & Schneider, D. (1995). Spatial variance in ecology. *Oikos*, 74, 18-26.

Jennions, M. & Petrie, M. (1997). Variation in mate choice and mating preferences: A review of causes and consequences. *Biol.Rev.Camb.Philos.Soc.*, 72, 283-327.

Koops, M. (2004). Reliability and the value of information. *Anim.Behav.*, 67, 103-111.

Koops, M. & Abrahams, M. (2003). Integrating the roles of information and competitive ability on the spatial distribution of social foragers. *Am.Nat.*, 161, 586-600.

Levin, S. (1992). The problem of pattern and scale in ecology. *Ecology*, 73, 1943-1967.

Lima, S. & Bednekoff, P. (1999). Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *Am.Nat.*, 153, 649-659.

McLinn, C. M. & Stephens, D. W. (2006). What makes information valuable: Signal reliability and environmental uncertainty. *Anim.Behav.*, 71, 1119-1129.

Navarrete, S. A., Broitman, B. R. & Menge, B. A. (2008). Interhemispheric comparison of recruitment to intertidal communities: Pattern persistence and scales of variation. *Ecology*, 89, 1308-1322.

Nichol, L. & Shackleton, D. (1996). Seasonal movements and foraging behaviour of northern resident killer whales (*Orcinus orca*) in relation to the inshore distribution of salmon (*Oncorhynchus spp*) in British Columbia, *Can.J.Zool.*, 74, 983-991.

Niven, J. E. & Laughlin, S. B. (2008). Energy limitation as a selective pressure on the evolution of sensory systems. *J.Exp.Biol.*, 211, 1792-1804.

Olsson, O. & Brown, J. (2006). The foraging benefits of information and the penalty of ignorance. *Oikos*, 112, 260-273.

Olsson, O. & Brown, J. S. (2010). Smart, smarter, smartest: Foraging information states and coexistence. *Oikos*, 119, 292-303.

Rieucau, G. & Giraldeau, L. (2011). Exploring the costs and benefits of social information use: An appraisal of current experimental evidence. *Philos. Trans. R. Soc. Lond. Ser. B* 366, 949-957.

Robb, G. N., McDonald, R. A., Chamberlain, D. E. & Bearhop, S. (2008). Food for thought: Supplementary feeding as a driver of ecological change in avian populations. *Front. Ecol. Environ.*, 6, 476-484.

Rose, G. & Leggett, W. (1988). Atmosphere ocean coupling and Atlantic cod migrations - effects of wind-forced variations in sea temperatures and currents on nearshore distributions and catch rates of *Gadus morhua. Can.J.Fish.Aquat.Sci.*, 45, 1234-1243.

Sanchez-Jerez, P., Fernandez-Jover, D., Uglem, I., Arechavala-Lopez, P., Dempster, T., Bayle-Sempere, T., *et al.*. (2011). Coastal fish farms as fish aggregation devices (FADs). In: *Artificial Reefs in fisheries Management* [Bortone, S., Brandini, R.P., Fabi, G., Otake, S.]}. CRC Press, Boco Raton, FL, USA, pp. 187-208.

Schneider, D. (2001). The rise of the concept of scale in ecology. *Bioscience*, 51, 545-553.

Sims, D., Witt, M., Richardson, A., Southall, E. & Metcalfe, J. (2006). Encounter success of free-ranging marine predator movements across a dynamic prey landscape. *Proc. Biol Sci.*, 273, 1195-1201.

Steele, J. (1991). Can ecological theory cross the land sea boundary? *J.Theor.Biol.*, 153, 425-436.

Stephens, D. (1989). Variance and the value of information. *Am.Nat.*, 134, 128-140.

Templeton, J.J. & Giraldeau, L.A. 1996. Vicarious sampling: the use of personal and public information by starlings foraging in a simple patchy environment. *Behav. Ecol. Sociobiol.* 38, 105-114.

Valone, T. (1989). Group foraging, public information, and patch estimation. *Oikos*, 56, 357-363.

Valone, T. & Brown, J. S. (1989). Measuring patch assessment abilities of desert granivores. *Ecology*, 70, 1800-1810.

Valone, T. (1992). Information for patch assessment - a field investigation with black-chinned hummingbirds. *Behav.Ecol.*, 3, 211-222.

Valone, T. (1991). Bayesian and prescient assessment - foraging with preharvest information. *Anim.Behav.*, 41, 569-577.

Valone, T. & Templeton, J. (2002). Public information for the assessment of quality: A widespread social phenomenon. *Philos. Trans. R. Soc. Lond. Ser. B* 357, 1549-1557.

van Gils, J. A. (2010). State-dependent bayesian foraging on spatially autocorrelated food distributions. *Oikos*, 119, 237-244.

Vasquez, R., Grossi, B. & Marquez, I. (2006). On the value of information: Studying changes in patch assessment abilities through learning. *Oikos*, 112, 298-310.

Ward, P. & Zahavi, A. (1973). Importance of certain assemblages of birds as information-centers for food-finding. *Ibis*, 115, 517-534.

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Res. II*, 54, 211-223.

Wiens, J. (1989). Spatial scaling in ecology. *Funct.Ecol.*, 3, 385-397.

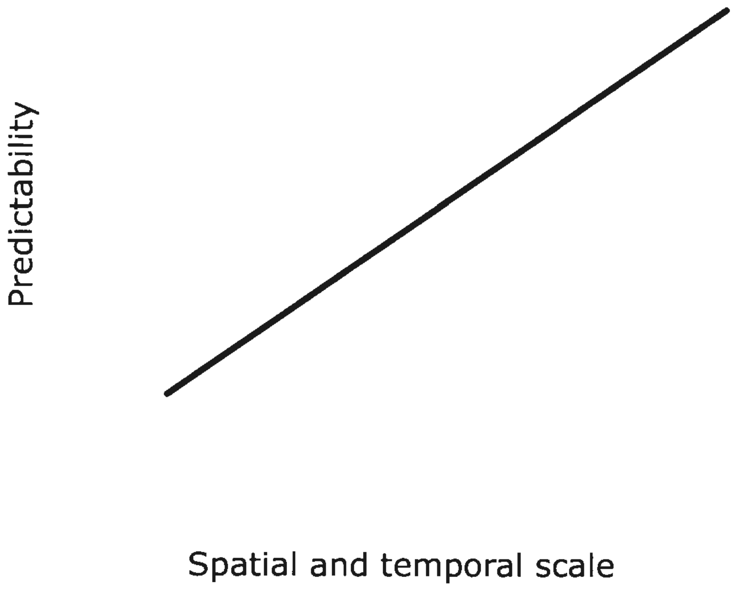

Figure 2.1. Theoretical relationship between environmental predictability and spatiotemporal scale. As the world is viewed through a progressively larger window of observation, predictability increases.

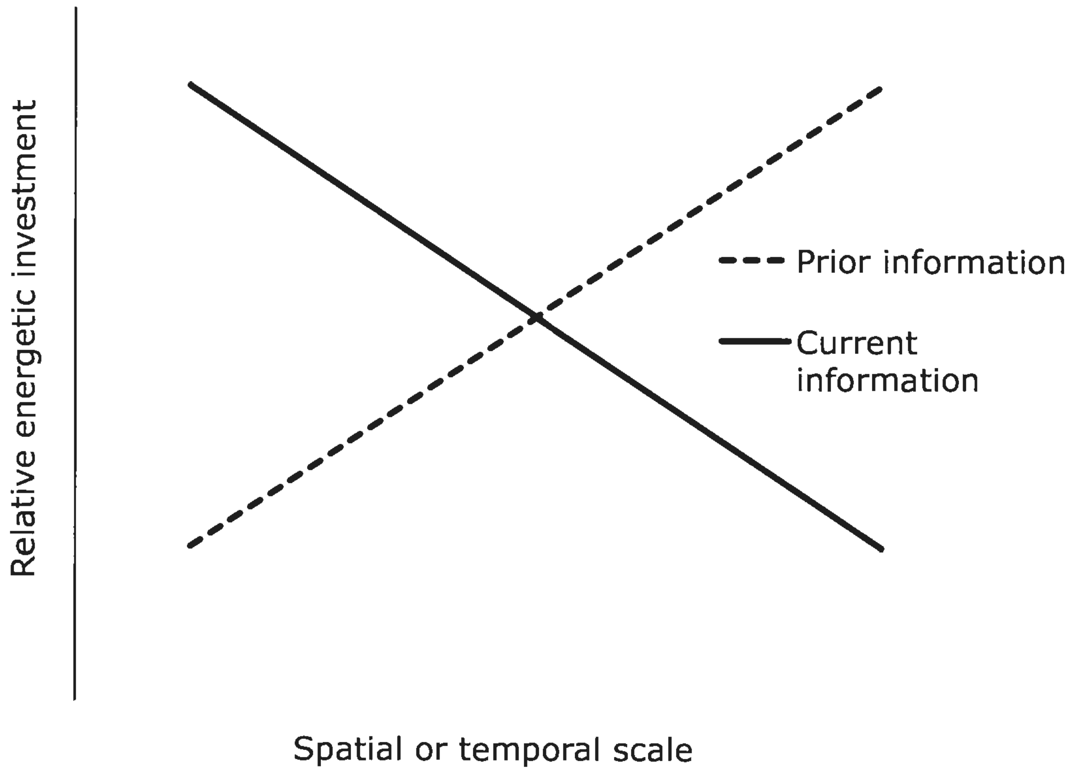

Figure 2.2. The relative amount of energy spent on current and prior information changes in relation to an animal's scale of experience. At large spatiotemporal scales, information is reliable, and energetic investments in prior information provide a pay off, thus favouring expensive information strategies that rely on prior information. At small scales of experience, less informed-and therefore less costly- strategies that rely more heavily on current information are effective and are more likely to be favoured amongst animals with small scales of experience.

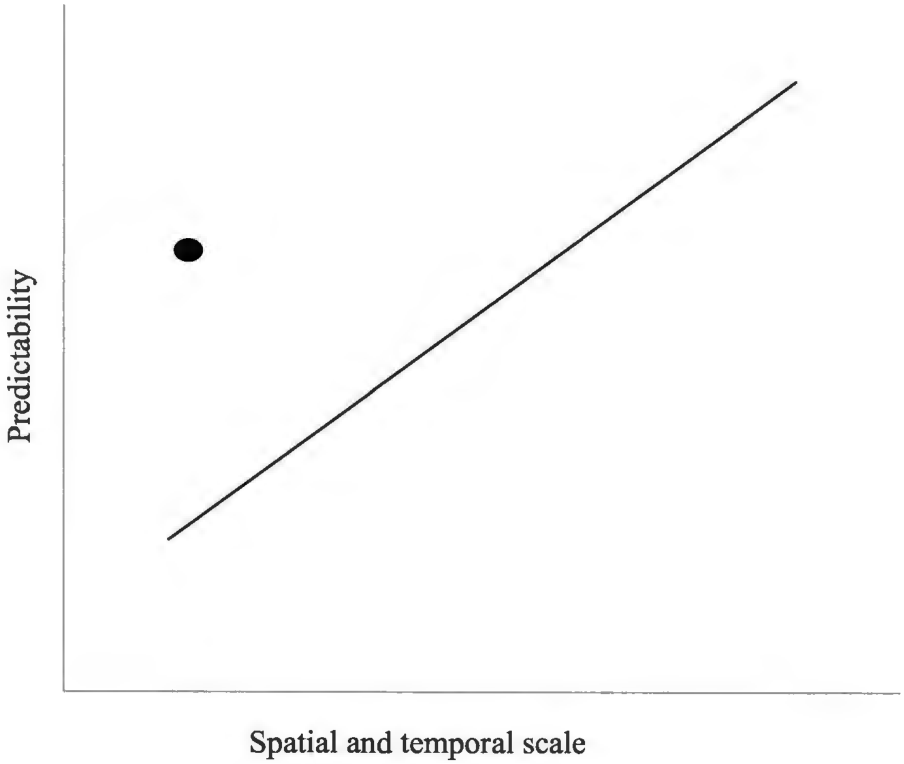

Figure 2.3. In the natural world, the predictability of patterned resource fluctuations increases with increasing spatial and temporal scale. The environmental impact of predictability occurs when sites are created in the environment that are generally fixed in space, and provide stable access to a resource in time (circle). As a consequence, they do not conform to the natural relationship between predictability and scale making it possible for animals to exploit a resource without investing in access to information

Chapter 3. Assessing the effects of environmental predictability on the perception of habitat quality

Livia Goodbrand[1*] and Mark V. Abrahams[1]

*[1] L. Goodbrand (Livia.Goodbrand@mun.ca), Department of Biology, Memorial University of Newfoundland, St. John's, NL, Canada A1C 5S7, Phone: (709)864-7493, Fax: (709)864-3316

[1]M.V. Abrahams, Department of Biology, Memorial University of Newfoundland

"Assessing the effects of environmental predictability" to be submitted as a research paper

Abstract

Organisms are adapted to variability in the availability of fluctuating biological and physical resources. Through anthropogenic activities, we often inadvertently diminished this variability by introducing resource patches into the environment that are highly predictable through space and time. I hypothesize that these predictable resource patches will be preferred over patches of equal value but that are variable, because animals can reduce the energetic costs of information at these sites. Using the Ideal Free Distribution as a tool for assessing habitat preference, I show that juvenile Atlantic cod (*Gadus morhua*) are able to quickly learn and develop a preference for predictable resource distributions. This preference is accompanied by a corresponding decrease in patch sampling behaviour, which supports the hypothesis that this preference is generated by the costs of obtaining information. I discuss this effect in the context of habitat change, and suggest that the study of predictability will become increasingly relevant as we consider the ways in which we impose predictability on the natural environment.

KEY WORDS: predictability, variability, information, ideal free distribution, habitat quality, environmental impact

Introduction

In stochastic environments, animals tend to make foraging decisions that minimize uncertainty. To be effective, a foraging decision must therefore integrate both variation and net rates of energy intake. The challenge of variance in making habitat selection decisions has been dealt with principally in the literature of 'risk sensitivity' (Caraco, 1980; Real 1980a,b; Stephens 1981; Houston and McNamara, 1982, 1985; McNamara and Houston, 1982, 1986, 1982; Pulliam and Millikan, 1982; Stephens and Charnov, 1982; Stephens and Krebs, 1986). Typically, an animal is forced to make a decision on where to forage based on its assessment of variation in the distribution of resources, and its decision is interpreted as a measure of the animal's energetic state. An animal operating on a positive energy budget should be risk adverse, and choose to minimize variance in its intake rate. A starved animal operating on a negative energy budget should accept the 'risk' of a variable intake rate, if its energy requirements cannot otherwise be met.

For animals that do not appear to follow the rules of risk sensitivity (see Kacelnik and Bateson, 1996) or for those whose metabolic state is relatively stable (e.g. cold water fish), variance in the distribution of resources is still a significant feature of the foraging environment. Spatial and temporal variability in the environment is a function of the spatial or temporal scale of our observation (Levin, 1992); thus at small spatial scales, i.e. the patch scale, resource distributions are variable. As the scale of observation is increased, there is a corresponding decrease in the variance of measured quantities (Figure 2.1). At very large scales, variance is minimal, and the world becomes a predictable place. It is reasonable to expect that the foraging strategies of animals are adapted to be effective at spatial and temporal scales that are biologically relevant at an individual level. These adaptations may be a response to the degree to which resources are predictable through space and time at that scale.

Whether an animal can perceive environmental predictability will depend on its ability to assess patch quality using memory (prior information) about the spatial and temporal distribution of resources (Valone, 1991). Animals that forage across large, predictable spatial-temporal scales, for example, seabirds (reviewed in Weimerskirch, 2007) and basking sharks (Sims et al, 2010), should be capable of using memory to assess patch quality, because information on the distribution of resources across large scales is reliable. Any animal that has access to reliable information can increase its individual rate of energy intake, relative to other individuals, by incorporating prior information into its assessment of patch quality (Valone 1992). This information, however, is expensive and the selection for traits that support such foraging strategies will depend on the balance between the costs and benefits of information (Olsson and Brown 2010). I suggest that the direction of this balance will be scale-dependent (Chapter 2).

What if the energetic costs of information were reduced and reliable information was available at small spatiotemporal scales? Many human activities inadvertently result in locally predictable resource patches, and these patches have become ubiquitous; for example, backyard bird feeders, sewage outflows, and sea cage aquaculture sites, all provide food to wild populations that is highly predictable, at small spatial and temporal scales. If animals can access information at an energetically 'discounted price' by foraging where resources have become predictable, then there may be a net value associated with foraging at these sites. I use the ideal free distribution theory (Fretwell and Lucas, 1970; Fretwell 1972), to assess the net value of a predictable resource patch, relative to a patch that is unpredictable, but of equal value. The results provide incentive for research in the area of resource predictability, and contribute to our understanding of how animals assess habitat quality in changing foraging environments.

Assessing the value of resource predictability

The ideal free distribution (IFD) theory (Fretwell and Lucas 1970; Fretwell 1972) has been used as a tool to investigate foraging decisions (e.g., Brown 1988; Abrahams and Dill 1989; Kotler and Blaustein 1995), and provides the testable prediction that for patches with continuous resource inputs, foragers should distribute themselves equally between resource patches of equal value, when competitive and perceptual abilities are assumed equal. Here, the distribution of juvenile Atlantic cod (*Gadus morhua*) and their patterns of resource use are compared to those predicted by the IFD with a continuous resource input to assess the preference for resource predictability in a generalist foraging marine fish. By manipulating only the predictability of food and not its value, I seek to demonstrate that fish will prefer the more predictable resource patch due to the reduced cost of using it.

Methods

Experimental Animals and Apparatus

Atlantic cod are cold water marine fish, with low standard and active metabolic rates (Tytler 1978; Schurmann and Steffensen 1997). They are unlikely to experience short, extreme shifts is their energetic state, and are therefore unlikely to display classic state-dependent foraging behaviour (risk sensitivity) within the timeframe of this experiment. Juvenile Atlantic cod (mean weight= 11.6g +/- 1.9 SD; total length= 10.7cm +/- 1.0 SD) were obtained from a domestic F1 generation stock, and kept in 358 L holding tanks at 9°C +/- 2°C for one week prior to the experiments. Holding tanks were identical to experimental tanks. Cod were maintained on a 12-h photoperiod and received *ad libitum* Skretting brand pellet feed for juvenile marine fish (1.5mm and 2.0mm) three times daily. I observed no competitive interactions between cod.

The experimental tank was a round 358 L flow-through tank, divided in half by 2 overlapping black Plexiglas sheets (Figure 3.1). Though fish were able to navigate between patches, the opaque dividers ensured that individuals were unable to compare food distributions between patches, except through patch sampling: fish were unable to see food being delivered into the other patch, and the dividers also prevented their ability to mechanically or chemically sense food availability. The ability of fish to navigate between the patches was tested in a preliminary experiment. Water inflow was diverted equally between both sides of the divider, and maintained at 25 L/hour per side.

Two 'Fish Mate' brand automated rotary aquarium feeders were located at opposite ends of the tank. Throughout a 10-hour feeding period, each feeder dispensed 1.3 g of pellet feed. The temporal distribution of feed was varied to establish a predictable and variable feeding patch. In the predictable patch, 0.13 g of food arrived every hour, between 08:00-18:00 hours. To induce temporal unpredictability, the amount of food that was dispensed each hour throughout the same 10-hour period was derived from a negative binomial distribution (mean=1.3 g/patch; variance=0.1). The negative binomial distribution was used for its large mean to variance ratio. A mesh screen was installed in the bottom of each tank to prevent cod from feeding on excess pellets.

Experimental procedure and assessment of fish distribution

Ten cod were introduced to the experimental tank and allowed to acclimatize for at least 2 days before beginning the feeding trials. Fish were fed *ad libitum* during acclimatization period. Each trial consisted of 5 experimental days, throughout which the distribution of cod was video recorded using an overhead Panasonic SD III video camera. The number of individuals located at the variable and predictable patch was recorded every 2 minutes for 20 minutes every hour, for eight hours per day. I considered the mean number of fish at the predictable patch per day as 1 independent sample for my analysis, which was taken from 24 observations per day. A total of nine replications of the experiment were run, yielding 45 independent samples.

The proportion of fish that were actively foraging at the predictable patch was considered in the analysis of patch use. Fish that were located between the patch dividers during an observation were recorded as 'not participating'.

Statistical analysis

Comparing patch use over time

For each experimental day, the average proportion of participating fish at the predictable patch was assessed. Although proportional data often require an arcsine square-root transformation to be normalized, a visual assessment of the residuals revealed no violation of the assumptions of normality, homogeneity, or independent errors. (Sokal and Rohlf 1995).

Therefore, the data were not transformed (Warton and Hui 2011), and were analysed as the effect of experimental day on the proportion of fish at the predictable feeder using a separate linear regression model for each of 9 replicate experimental trials. The hypothesis that the proportion of fish at the predictable patch increased over time was tested against a null hypothesis of no change by comparing the observed slopes to a predicted slope of 0, using a one-tail t-test.

Comparing patch use to the Ideal Free Distribution theory

The IFD predicts that fish should distribute themselves equally between patches of equal value. In this experiment, patches differed only in the temporal distribution of food, not in the quantity of food available per day; thus the fish should distribute themselves evenly between the two patches. The observed distribution of fish was compared to the IFD using an independent t-test for each experimental day.

Evaluating patch sampling through time

Patch sampling was quantified as the standard deviation in daily fish distribution data. Variability in the observed distribution of fish can be the result of two sources: the proportion of fish feeding at either patch can change between observations, and the number of participating fish can change between observations. As participation rate was found to be high (μ=0.95 +/- 0.02 S.E.) and did not differ statistically throughout the experimental trials ($t_{1,8}$= 1.92; p= 0.091), variability was attributed to changes in the proportion of fish at the predictable patch between observations. I ran a separate linear regression model for each of 9 independent trials. I compared the observed slopes to a predicted slope of 0 (no change in patch sampling over time) using a one-tail t-test.

Results

Comparing patch use over time

I hypothesized that cod would increase their preference for the predictable patch over the 5 experimental days, which was tested against a null hypothesis of no change. The proportion of fish at the predictable patch increased throughout the 5-day experimental trials ($t_{1,8} = 3.59$; $p<0.005$). On the final day of the experiment, the proportion of fish at the predictable patch was slightly lower than on experimental day 4, but the variability was greatly reduced (Figure 3.2).

Comparing patch use to the Ideal Free Distribution theory

The distribution of fish did not deviate from the IFD on experimental day 1, but fish began to develop a preference for the predictable patch as early as 2 (Figure 3.2). By day 3, the difference between observed and predicted patch use was significant.

Evaluating patch sampling through time

Patch sampling, which was quantified as the standard deviation in the distribution of fish at the predictable patch, decreased throughout the 5-day experimental period (Figure 3.3). This change was significant across all 9 independent trials ($T_{1,8} = -3.58$; $p<0.05$)

Discussion

According to the IFD theory (Fretwell and Lucas 1970; Fretwell 1972), foragers should distribute themselves equally between patches of equal value. In this experiment, an equal amount of food was available per day at predictable and variable patches, but the patches differed in the temporal availability of the food items. The proportion of cod at the predictable patch increased over time and by experimental day 3, the distribution of cod deviated significantly from the IFD. Patch sampling behaviour decreased simultaneously with increasing use of the predictable patch throughout the 5-day experimental trials. The cod apparently learned the distribution of resource through intense patch sampling at the beginning of the trial, before committing to foraging at the predictable patch. This study provides experimental evidence that foragers prefer resource distributions that are predictable through time, to those that are of equal value but unpredictable. This preference may be attributed to a reduction in the energetic cost of patch assessment at the predictable patch.

Predictability in the distribution of resources can affect both the 'ideal' and 'free' assumptions of the IFD. When foraging in spatially unpredictable environments, Grand and Grant (1994a) found that the distribution of convict cichlids, *Cichlasoma nigrofasciatum*, deviated from the IFD, but was consistent with the perceptual constraints model (Abrahams 1986); individuals were unable to track the distribution of unpredictable resources, and on average, underused good patches while overusing poor patches. When resources were spatially predictable, dominant fish monopolized resources by excluding subordinates from the best patches, and their distribution was consistent with the Ideal Despotic Distribution (Fretwell

1972) (Grand and Grant 1994a). In general, the introduction of a predictable patch causes an increase in aggressive behaviour (Grand and Grant 1994b; Goldberg et al 2001) because predictable resource distributions are more economically defensible (Grant 1993). I did not observe significant competitive interactions between my experimental cod, so it was assumed that any deviation from the IFD was due to their ability to learn the temporal distribution of resources. I show that when given a choice between two patches of equal value, the distribution of juvenile cod deviates from the IFD because individuals prefer to forage where they can acquire 'perfect' knowledge of their environment.

Animals foraging in natural systems are encountering predictable resource patches, and the results of this study suggest that animals will prefer to forage where they can save energy on costs of information. Thus we should expect to see an overuse of resource patches that are predictable through space and time, regardless of patch quality. Many such sites exist, but have yet to be studied in the context of resource predictability. For example, large, multi-species assemblages of wild fish often associate with sea cage aquaculture sites (Sanchez-Jerez et al 2011), where excess feed pellets become available regularly throughout the day, over periods of 2-4 years.

The study of resource predictability will become increasingly relevant as we consider the ways in which we impose predictability on the natural environment. To survive in highly variable environments, many organisms have adapted to exploit fluctuating resource availabilities opportunistically. For example, by having broad diet breadths (MacArthur and Levins 1967; MacArthur 1975; reviewed in Futuyama and Moreno 1988); by responding quickly to the nutrients that are available (e.g. Kiorboe et al 1985); and by using information on habitat quality to make foraging decisions (for example McNamara and Houston 1980; Stephens and

Krebs 1986; Valone and Brown 1989; for general review see Giraldeau 1997), animals cope with heterogeneity and local stochasticity in the distribution of food. Changes to habitats that diminish variability should have a profound environmental effect because variability defines the life histories of many organisms. If, as I suggest, animals prefer to forage where resource distributions have become predictable, then we should expect to see changes in the distribution of wild animals in response to the introduction of predictable resource patches. Understanding the consequences of this behaviour will be important for predicting the outcome of habitat change for individual, community, and ecosystem-level responses.

Acknowledgments

I wish to acknowledge I. Fleming, C. Purchase, D. Bassett, J. Mitchell, and other colleagues at the Ocean Sciences Center for their thoughtful contributions. Technical support and advice was provided by D. Boyce at the Joe Brown Aquatic Research Building and staff at the Ocean Sciences Center. Experimental animals were provided by the Atlantic Cod Genomics and Broodstock Development Program. Financial support was provided by a Memorial University Graduate Fellowship to L. Goodbrand and by NSERC, Memorial University, and Newfoundland Research Development Corporation Grants to M. Abrahams.

References

Abrahams, M. 1986. Patch choice under perceptual constraints - a cause for departures from an Ideal Free Distribution. Behavioral Ecology and Sociobiology, 19, 409-415.

Abrahams, M. & Dill, L. 1989. A determination of the energetic equivalence of the risk of predation. Ecology, 70, 999-1007.

Brown, J. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology, 22, 37-47.

Caraco, T. 1980. On foraging time allocation in a stochastic environment. Ecology, 61, 119-128

Fretwell, S.D. 1972. *Populations in a seasonal environment.* Princeton, New Jersey: Princeton University Press.

Fretwell, S.D. & Lucas, H.L. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica, 19, 16-36 .

Futuyma, D.J. & Moreno, G. 1988. The evolution of ecological specialization. A. Rev. Ecol. Syst. 19, 207-233.

Giraldeau, L.A. 1997. The ecology of information use. In *Behavioural ecology* (ed. J.R. Krebs & N.B. Davies), pp. 42-68. London: Blackwell.

Goldberg, J., Grant, J. & Lefebvre, L. 2001. Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. Behavioral Ecology, 12, 490-495.

Grand, T. & Grant, J. 1994. Spatial Predictability of Resources and the Ideal Free Distribution in Convict Cichlids, Cichlasoma-Nigrofasciatum. Animal Behaviour, 48, 909-919.

Grand, T. & Grant, J. 1994. Spatial predictability of food influences its monopolization and defense by juvenile convict cichlids. Animal Behaviour, 47, 91-100.

Grant, J. 1993. Whether or not to defend - the influence of resource distribution. Marine Behaviour and Physiology, 23, 137-153.

Houston, A. & Mcnamara, J. 1982. A sequential approach to risk-taking. Animal Behaviour, 30, 1260-1261.

Houston, A. & Mcnamara, J. 1985. A general-theory of central place foraging for single-prey loaders. Theoretical Population Biology, 28, 233-262.

Kacelnik, A. & Bateson, M. 1996. Risky theories - The effects of variance on foraging decisions. American Zoologist, 36, 402-434.

Kiorboe, T., Mohlenberg, F. & Hamburger, K. 1985. Bioenergetics of the planktonic copepod *Acartia tonsa* - Relation between feeding, egg-production and respiration, and composition of specific dynamic action. Marine Ecology-Progress Series, 26, 85-97.

Kotler, B. & Blaustein, L. 1995. Titrating food and safety in a heterogeneous environment: When are the risky and safe patches of equal value? Oikos, 74, 251-258.

Levin, S. 1992. The problem of pattern and scale in ecology. Ecology, 73, 1943-1967.

MacArthur, J.W. 1975. Environmental fluctuations and species diversity, In: *Ecology and evolution of communities* (Ed. by M.L. Cody and J.M Diamond), pp. 74-80 Belknap Press, Cambridge, Massachusetts, USA.

MacArthur, R.,& Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist, 101, 377-385

McNamara, J.M. & A.I. Houston. 1982. Short-term behaviour and life-time fitness. In: *Functional Ontogeny*, (Ed. by D. J. McFarland), pp. 60-87. London: Pitman.

Mcnamara, J. & Houston, A. 1992. Risk-sensitive foraging - a review of the theory. Bulletin of Mathematical Biology, 54, 355-378.

Mcnamara, J. & Houston, A. 1986. The common currency for behavioral decisions. American Naturalist, 127, 358-378.

Olsson, O. & Brown, J. S. 2010. Smart, smarter, smartest: foraging information states and coexistence. Oikos, 119, 292-303.

Pulliam, H.R. &G.C. Millikan. 1982. Social organization in the non-reproductive season. In: *Avian Biology*, Vol. 6 (Ed. By D.S. Farmer, J.R. King and K.C. Parked), pp. 169-197. New York: Academic Press.

Real, L. 1980a. On uncertainty and the law of diminishing returns in evolution and behaviour. In: *Limits to action: The allocation of individual behaviour* (Ed. By J.E.R. Staddon), pp. 37-64. Academic Press, New York.

Real, L. 1980b. Fitness, uncertainty, and the role of diversification in evolution and behavior. American Naturalist, 115, 623-638.

Sanchez-Jerez, P., Fernandez-Jover, D., Uglem, I., Arechavala-Lopez, P., Dempster, T., Bayle-Sempere, T., *et al.* 2011. Coastal fish farms as fish aggregation devices (FADs). In: *Artificial Reefs in fisheries Management* (Ed. By S. Bortone, R.P. Brandini, G. Fabi, & S. Otake), pp. 187-208CRC Press, Boco Raton, FL, USA.

Schurmann, H. & Steffensen, J. 1997. Effects of temperature, hypoxia and activity on the metabolism of juvenile Atlantic cod. Journal of Fish Biology, 50, 1166-1180.

Sims, D., Witt, M., Richardson, A., Southall, E. & Metcalfe, J. 2006. Encounter success of free-ranging marine predator movements across a dynamic prey landscape. Proceedings of the Royal Society B-Biological Sciences, 273, 1195-1201.

Stephens, D. 1989. Variance and the value of information. American Naturalist, 134, 128-140.

Stephens, D. 1981. The logic of risk-sensitive foraging preferences. Animal Behaviour, 29, 628-629.

Stephens, D. & Charnov, E. 1982. Optimal foraging - some simple stochastic-models. Behavioral Ecology and Sociobiology, 10, 251-263.

Stephens, D.W. & J.R. Krebs. 1986. Foraging theory. Princeton, New Jersey: Princeton University Press.

Tytler, P. 1978. The influence of swimming performance on the metabolic rate of gadoid fish. *In: Physiology and Behaviour of Marine Organisms (Ed. by D.S.* McLusky, D *& A.J.* Berry*), pp.* 82–93. *Oxford : Pergamon Press.*

Valone, T. 1992. Information for patch assessment - a field investigation with black-chinned hummingbirds. Behavioral Ecology, 3, 211-222.

Valone, T. 1991. Bayesian and prescient assessment - foraging with preharvest information. Animal Behaviour, 41, 569-577.

Valone, T. & Brown, J. 1989. Measuring patch assessment abilities of deserg granivores. Ecology, 70, 1800-1810.

Warton, D. & Hui F. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology, 92(1), 3-10.

Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? Deep-Sea Research Part II-Topical Studies in Oceanography, 54, 211-223.

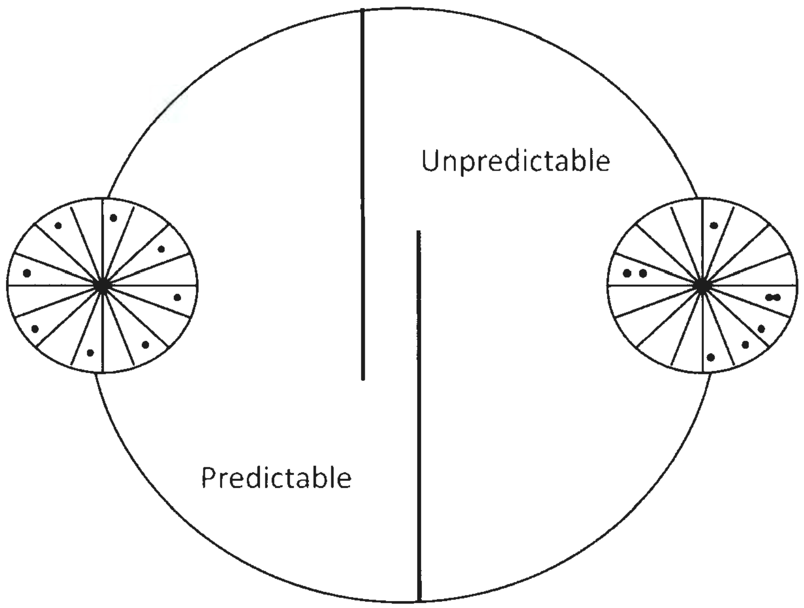

Figure 3.1. Schematic illustration of experimental tank design. Two resource patches are created with opaque Plexiglass dividers that allow fish to move between patches, but that do not allow for the visual, mechanical, or chemical detection of resource availability between patches. Using rotary feeders, an equal amount of food is delivered at each patch throughout the day, but the temporal distribution of food in a patch is either predictable or unpredictable.

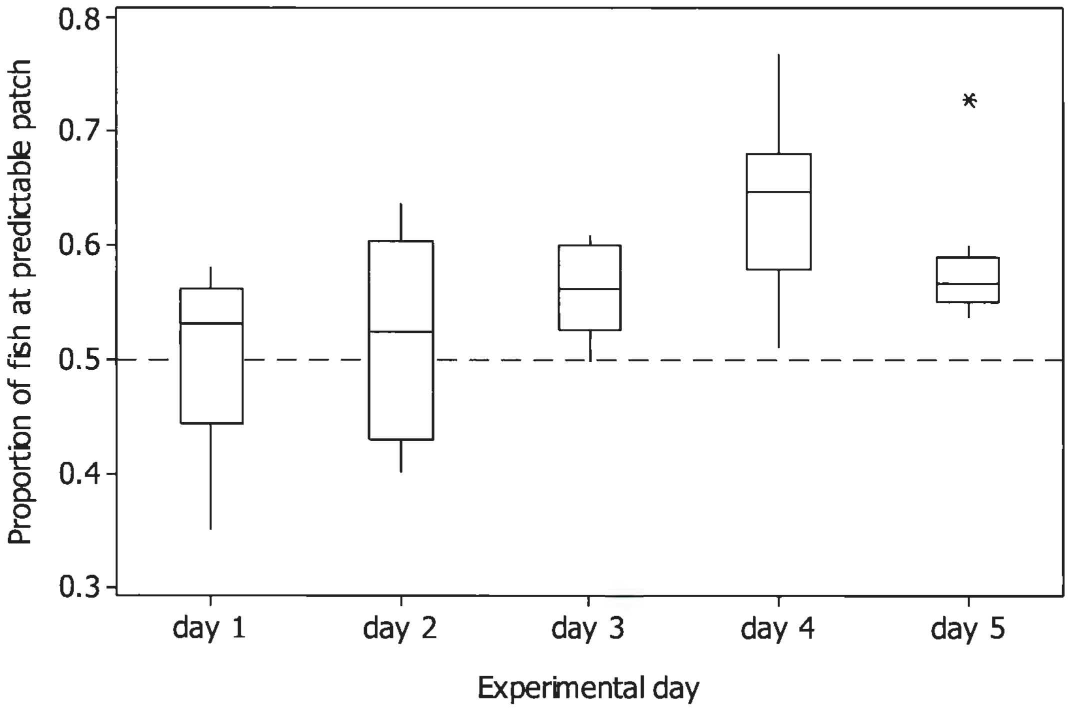

Figure 3.2. The proportion of fish at the predictable patch for each of five experimental days (n=9 trials per experimental day). Boxplots show median, interquartile range, and upper and lower 10th percentiles. Outliers shown as stars. Distribution of fish predicted by the Ideal Free Distribution (0.5) shown as stippled line.

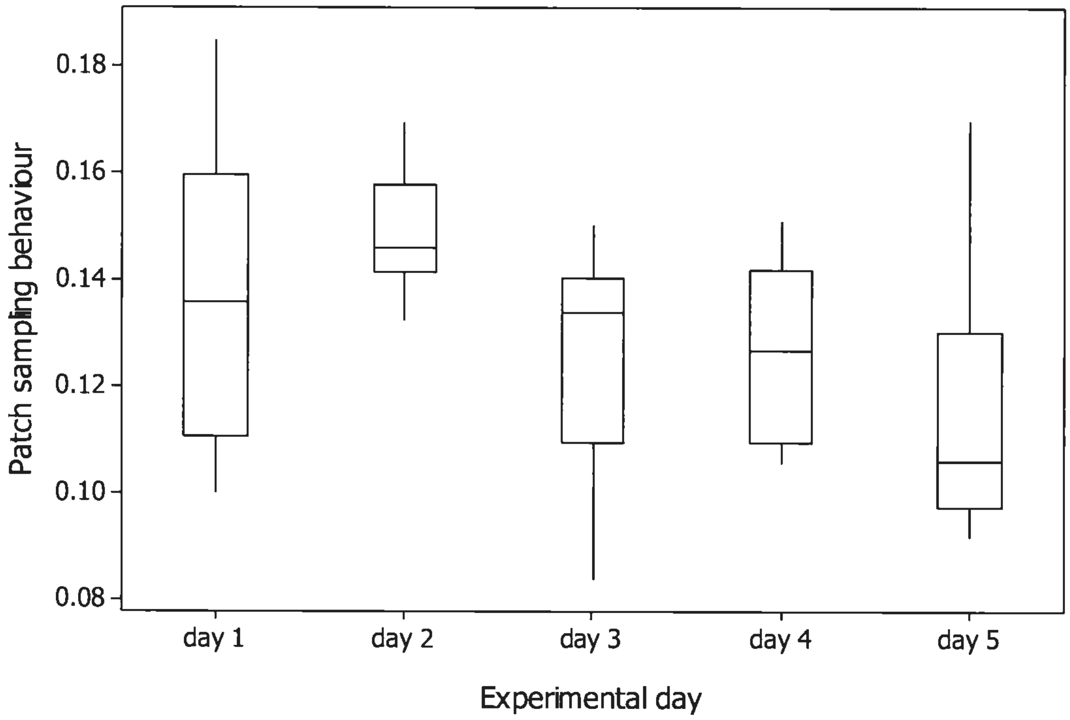

Figure 3.3. Patch sampling decreases throughout the five day experimental period. Patch sampling is quantified as the standard deviation of the number of fish at the predictable patch. Boxplot shows median, inter quartile range, and upper and lower 10th percentiles.

Chapter 4. Introducing predictability to coastal marine environments: the effect of aquaculture on wild fish distributions.

Goodbrand, L.[1]*, M. Abrahams[1], & G. Rose[2]

*[1] L. Goodbrand (Livia.Goodbrand@mun.ca), Department of Biology, Memorial University of Newfoundland, St. John's, NL, Canada A1C 5S7, Phone: (709)864-7493, Fax: (709)864-3316

[1]M.V. Abrahams (Mabrahams@mun.ca), Department of Biology, Memorial University of Newfoundland, St. John's, NL

[2] G.Rose (George.Rose@mi.mun.ca), Center for Fisheries and Ecosystem Research, Fisheries and Marine Institute of Memorial University, St. John's, NL

"Introducing predictability" to be submitted as a research paper

Abstract

Aquaculture sea cages are fixed in space and inadvertently provide food to wild animals that is stable through time. Sea cages therefore act like predictable resource patches in an otherwise stochastic foraging environment. I measured the effect of these novel and highly predictable resource patches on the distribution of marine life across large spatial scales along the South coast of Newfoundland, Canada. Randomized stratified hydroacoustic surveys were used to compare the distribution and abundance of marine life in bays that contained salmon farms, to control bays. Control bays were areas with no history of aquaculture, but which have been selected for future use by the salmon farming industry. I used nautical area scattering coefficient (NASC) as my measure of total area backscatter, and found bays containing salmon farms had significantly greater biological activity compared to control locations. The mean NASC throughout farmed bays was not significantly different from mean NASC measurements taken directly adjacent to sea cages. Variability around mean estimates could not be explained by the quantity of feed available to consumers, when the number of sea cages in a farm site were used as a proxy for feed availability. My results suggest that consumer responses at the individual-level can be transmitted across the larger community.

Key words: predictability, scale, aquaculture effects, distribution

Introduction

Aquaculture sea cage sites are often located in the same place for multiple years, and fish within these sea cages are fed on a regular schedule through time. Excess or lost feed drifts outside of sea cage nets, and meals intended for farmed fish inadvertently become available to wild organisms (Fernandez-Jover et al, 2007, 2008). In this way, sea cages act as novel resource patches for foraging marine animals. Compared to locations of equivalent size within coastal marine environments, sea cages are abnormal in that they are highly predictable patches in an otherwise stochastic seascape (Cloern and Jassby 2008; 2010). In areas of intense aquaculture, the result has been the creation of a novel patch landscape in which patterns of variability in the distribution of resources have become highly predictable through time and space.

For animals that have adapted to spatial and temporal variability in distribution of resources, changes that act to diminish variability should have a profound effect on individual and community-level consumer responses. One effect of introducing sea cages into marine environments has been the attraction of wild fish. Using diver-based SCUBA surveys (Dempster et al, 2002, 2004, 2005; Boyra et al, 2004; Tuya et al, 2006; Fernandez-Jover et al, 2008, 2009; Valee et al, 2006; Vita et al, 2004; Oakes and Pondella, 2009; Katz et al, 2002) or stationary video recordings (Dempster et al, 2009, 2010), the attractive area of a fish farm has been shown to include waters directly below and adjacent (within 5 m) to sea cages (e.g. Dempster et al 2009). The biomass and composition of these wild fish aggregations can vary between sites (Dempster et al, 2002, 2005) and sampling periods (Dempster et al, 2002; Fernandez-Jover et al, 2008), but a global trend has emerged: aggregations of wild fish at aquaculture sea cage sites are large, diverse, and persistent (Sanchez-Jerez et al, 2011). In areas where multiple farms operate in close proximity, the attraction of wild fish to sea cages has been described as an "ecosystem effect" (Dempster et al 2009), which considers the sum of localized wild fish aggregations (within 5 m) at multiple farm sites.

Whether and how individual-level consumer responses at sea cages initiate bottom-up effects at the community or ecosystem-level have not been tested. To determine whether the effect of coastal marine aquaculture is greater than the sum of local aggregations at individual farm sites, new methods are needed to assess the community-level response of wild fish populations to these novel foraging environments. In this study, I use hydroacoustic techniques to compare the large-scale distribution and abundance of marine organisms in bays containing salmon farms to control bays. I hypothesize that the energetic advantages of foraging at sea cages results in a large-scale redistribution of biological activity into bays that support sea cage aquaculture. The effect of coastal marine aquaculture on marine life is discussed within the context of habitat change that acts to reduce spatial and temporal variability in naturally stochastic environments.

Methods

Study Sites

Acoustic surveys were conducted along the southern coast of Newfoundland (Figure 4.1), where commercial salmon farming has become an important developing industry (DFA 2010). A total of 8 farm bays and 5 control bays were surveyed (Table 4.1). Each farm bay contained 1 or multiple farm sites, and farm sites were composed of 8-16 active (i.e., producing salmon) sea cages. All sea cages were round (10 m diameter), approximately 20 m deep, and contained salmon ranging from post-smolts to market-size salmon. Since the Newfoundland aquaculture industry is in a period of development, farming has not yet expanded into all suitable bays in the region. With the exception of 1 control bay that had previously supported salmon farming 3 years ago, control bays are in areas that have been selected for future use, but have no history of aquaculture.

Sampling Procedure

For both farm and control bays, line transects were oriented parallel to the head of each bay and were selected according to a randomized stratified survey design. For acoustic surveys of marine fish, a stratified randomized transect design can provide more precise estimates of mean and variance, compared to a completely randomized design (Jolly and Hampton, 1990; Simmonds and Fryer, 1996). Since inner and outer-bay habitats can be oceanographically distinct (e.g. Abookire et al 2000), stratification can also account for important biological differences between inner and outer bay areas. Beginning at the head of each bay, I systematically divided bays into 1-km long strata. Strata were subdivided into 100 parallel 10-m segments that crossed the full width of the bay, and were sequentially numbered. For each strata, 3 parallel transects were randomly selected from the 100 segments for sampling. Thus transects were randomly chosen within systematic strata (Figure 4.2a). This design allowed me to proportionally allocate sampling effort: large bays containing multiple strata were guaranteed a larger sampling effort. Surveys in small bays (1 km) that contained only 1 stratum were effectively random.

Since dense wild fish aggregations have been observed directly below and adjacent (within 5 m) to sea cages (e.g. Dempster et al 2009), I wanted to assess the abundance and distribution of wild fish within 5 m of sea cages independently from my stratified random transect design. Where salmon farms occurred, linear transects were surveyed to estimate wild fish abundance underneath and immediately adjacent to sea cages (Figure 4.2b). Given the conical shape of the acoustic beam, I was able to effectively detect fish beneath the periphery of sea cages, but not beneath the center of cages. Sea cages and fish inside sea cage nets (i.e. farmed salmon) were excluded from analysis.

Acoustic data were collected over a period of 3 days in September 2011 aboard a small (10 m) vessel, 'The Gecho II'. Measurements of volume-backscattering strength (Sv) were made with a calibrated 38 kHz echosounder (Simrad EK500) and a split beam ES38B transducer mounted on an extendable arm (see Appendix 1 for settings).

Analysis

The acoustic data were analysed using Echoview software (Version 6; Myriax Inc., Hobart, Australia). Data were analyzed within a range from the seabed to 5 m from the transducer. Non-biological signals (e.g. ropes) were identified and excluded from the analysis. Total backscatter was integrated over each transect at a threshold of -70 dB and then converted to nautical area scattering coefficient (NASC), defined as the area backscattering strength per nautical mile (Simmonds and MacLennan 2005).

Nautical area scattering coefficient values were ln-transformed to meet the assumptions of normal, heterogeneous, and independent errors for ANOVA (goodness-of-fit Kolmogorov-Smirnov test, $P > 0.05$). In order to make comparisons between locations using each bay as one independent observation, I reconstructed estimates of mean and standard error for each bay from my randomized stratified sampling design. Within stratum estimates of mean NASC and spatial variance were calculated from the 3 random transects. To generate one estimate of mean NASC and standard error for each bay, I took the population mean and the sum of standard errors from all strata within each bay. I then tested for differences in mean NASC between farm and control bays, using a one-way ANOVA.

Although the amount of food delivered to each sea cage may vary, I considered the number of sea cages within a farm site as a proxy for the quantity of feed lost to the environment. Since each farm bay contained 1+ farm sites, and farm sites were composed of a variable number of active cages (i.e. those that contained farmed salmon), I tested to see if there was a positive relation between cage number and mean NASC using a linear regression model. Similarly, for transects around sea cages I used a linear regression model to test the effect of cage number on mean NASC within farm sites.

Results

My survey design was stratified to account for potential biological differences between inner and outer bay habitats. Since I found no evidence that estimates of mean NASC differed between strata ($F_{2,57}= 0.15$; $p=0.865$), I integrated the variation amongst strata into my estimate of NASC within each bay.

Mean NASC was significantly greater in bays that contained salmon farms, compared to control bays ($F_{1,12}=53.18$; $p<0.001$, see Figure 4.3). Visual inspection of the echograms suggests that the main biological contributions to NASC in farm bays and at farm sites were schools of small pelagic fish, within the known range of acoustic target strengths of Atlantic herring (*Clupea harengus*) (see Simmonds and McLennan 2005 and references therein) and more diffuse groups of larger demersal fish, consistent with the target strength of Atlantic cod (*Gadus morhua*) (Rose and Porter 1996). Local fishermen confirmed the presence of cod aggregations and large schools of herring at the time of my surveys. I did not find evidence of Atlantic salmon (*Salmo salar*) in my analysis of the echograms.

Mean NASC was measured using linear transects at 11 farm sites. Each farm bay contained 1 or multiple farm sites, and each farm site was composed of 8-16 operational sea cages. There was a large magnitude of variability around mean NASC estimates at sea cages, which could not be explained by the number of active sea cages ($F_{1, 10}$= 0.22; p=0.648). Differences in mean NASC between farm bays were also unrelated to the total number of sea cages operating within each bay ($F_{1,7}$= 1.77; p=0.232). Despite considerable variability in mean NASC estimates between farm sites, there was no difference in the amount of biological activity observed directly adjacent to and below sea cages, compared to the larger farm bay environment (Figure 4.3).

Discussion

I demonstrate that introducing a point source resource patch that is highly predictable into a naturally stochastic environment can enhance biological activity across large spatial scales. Consistent with previous video and SCUBA surveys at aquaculture sites, I detected large abundances of wild fish below and adjacent to sea cages (reviewed Sanchez-Jerez et al 2011). Using hydroacoustics survey methods, however, my data indicate that the attractive area around sea cage sites is not limited to a 5 m 'attractive farm area' previously described (see Dempster et al 2009). Instead, I find evidence that sea cage aquaculture can enhance biological activity within the larger farm bay environment. Thus the 'ecosystem effect' of coastal marine aquaculture can be greater than the sum of wild fish aggregations at individual farm sites.

Apparently, this effect is not dependent on the amount of pellet food entering the environment. Although I did not measure feed loss directly, I considered the number of sea cages to be a useful proxy for the amount of excess pellet food available to wild organisms. I found no effect of cage number on the abundance of biological activity at farm sites, nor within the larger farm bay. Similarly, Dempster et al (2009) was unable to associate variability in the biomass of wild fish aggregations in Norway to the stocking density of sea cages (as a proxy for the amount of feed loss). The authors offered two explanations for their finding: either the amount of feed loss is unrelated to the amount of feed entering a cage (stocking density), or some farm sites may be located in closer proximity to biologically important habitats for wild fish (Dempster et al 2009). Since I observed enhanced biological activity within the larger farm bay environment, and variability at the bay scale was not attributed to cage number, I suggest that bottom-up effects may offset the direct impact of pellet feed quantity at sea cages.

I suggest that this community-level effect be considered within the broader context of environmental change that acts to reduce variability in patterns of fluctuating resources. Since variability tends to decay at increasingly large spatiotemporal scales (Wiens 1989; Levin 1992), predictability is a feature of patterned environmental fluctuation that is normally observed at large temporal and spatial scales. The introduction of a site into the environment that is fixed in space and provides stable access to a resource in time represents a fundamental change for animals that have adapted to this natural relationship between variability and scale. For these animals, the energetic advantage of foraging where patterns in the distribution of fluctuating resources have become predictable may be greater than the energetic value associated with the quantity of food alone. Indeed, fish that associate with sea cages have higher total body fat and higher body condition, relative to non-cage associated wild fish (Fernandez-Jover et al 2007; Dempster et al 2011).

This energetic advantage predicates the mechanisms that could allow for the effects of sea cage aquaculture to be transmitted across large spatial scales: (1) the conversion and storage of pellet feed into resident wild fish biomass; (2) the attraction of consumers at higher trophic levels that feed on resident fish biomass; (3) the movement of consumers between farm sites within the larger farmed landscape in response to increased competition or predation. Upon introducing sea cages into the environment, the mechanisms may proceed sequentially: the first impact may be the attraction of locally occurring fish populations, followed by an attraction of mobile opportunistic piscivores that feed on the resident fish biomass. The spatial and temporal stability of the farm system (cages remain in place for a period of 3-4 years), is likely to introduce density-dependent risks to the sea cage habitat, forcing individuals to move between sites. Once a site has become established, the 3 mechanisms can act simultaneously to enhance the total biological activity within the larger bay environment.

The community-level effect that I observed in response to the introduction of a predictable resource patch is not unique to sea cage aquaculture. An increasing number of studies from a variety of natural systems suggest that many human activities act to reduce environmental variably. For example, backyard bird feeders (reviewed in Robb et al 2008), sewage outflows (e.g. Fuller and Glue 1980; Park and Cristinacce 2007), fishery discards (e.g. Grémillet et al 2008; Cama et al 2011), and garbage dumps (e.g. Badyaev 1998; Cortes-Avizanda et al 2011), all provide food resources to wild animals that are predictable through space and time. In order to compare consumer responses across multiple habitat types, we must first consider how these responses may differ independently from the quantity of food introduced. Whether consistent patterns of effect can be observed in response to predicable resource distributions will provide insight into the structure, function, and stability of community-level processes and interactions.

As a starting point, I suggest that consumer responses to predictable resource distributions are conceptually similar to those responses that follow a resource pulse (reviewed in Yang et al 2008). Unlike resource pulses, which are defined as infrequent periods of resource availability that are intense and short in duration (Yang et al 2008), predictable resource patches provide food availabilities that are frequent, intense, and persistent through space and time. As a result, the magnitude of effect may be greater at predictable resource patches, because predictable distributions can be learned and continually exploited. This effect has been demonstrated in studies of resource pulses, as the duration of consumer responses increases with longer resource pulse durations (Yang et al 2010). In turn, persistent high densities of individuals at these sites may become predictable prey themselves (prey hotspots, Sih 2005; Roth and Lima 2007) or facilitate the spread of disease (host-density effects, see Arneberg et al, 1998; Arneberg 2001, 2002). Given the expansion of aquaculture and other anthropogenic activities that act to diminish environmental variability, it would be prudent to develop a frame-work for understanding the general effects of this change for animals that are adapted to cope with and exploit a naturally variable world.

Acknowledgments

This research was made possible through collaborations with the Newfoundland Aquaculture Association, Northern Harvest Sea Farms, and the Center for Fisheries Ecosystems Research. Logistical and technical support was provided by G. Adams and W. Hiscock at the CFER. My thanks to J. Caines and D. Caines at NHSF for support and local expertise. Financial support was provided by a Memorial University Graduate Fellowship to L. Goodbrand and by NSERC, Memorial University, and Newfoundland Research Development Corporation Grants to M. Abrahams.

References

Abookire, A.A, Piatt, J.F. & M.D. Robards. (2000). Near shore fish distribution in an Alaskan estuary in relation to stratification, temperature and salinity. Estuarine, Coastal and Shelf Science, 51, 45-59.

Arneberg, P. (2002). Host population density and body mass as determinants of species richness in parasite communities: Comparative analyses of directly transmitted nematodes of mammals. Ecography, 25, 88-94.

Arneberg, P. (2001). An ecological law and its macroecological consequences as revealed by studies of relationships between host densities and parasite prevalence. Ecography, 24, 352-358.

Arneberg, P., Skorping, A., Grenfell, B. & Read, A. (1998). Host densities as determinants of abundance in parasite communities, Proc. Roy. Soc. Lond. Ser. B, 265, 1283-1289.

Badyaev, A. (1998). Environmental stress and developmental stability in dentition of the Yellowstone grizzly bears. Behavioural Ecology, 9, 339-344

Boyra, A., Sanchez-Jerez, P., Tuya, F., Espino, F. & Haroun, R. (2004). Attraction of wild coastal fishes to an atlantic subtropical cage fish farms, Gran Canaria, Canary Islands. Environ.Biol.Fishes, 70, 393-401.

Cama, A., Abellana, R., Christel, I., Ferrer, X., Vietes, D. (2012). Living on predictability: modeling the density distribution of efficient foraging seabirds. Ecography, 35, 001-010

Cloern, J. E. & Jassby, A. D. (2010). Patterns and scales of phytoplankton variability in estuarine-coastal ecosystems. Estuaries and Coasts, 33, 230-241.

Cloern, J. E. & Jassby, A. D. (2008). Complex seasonal patterns of primary producers at the land-sea interface. Ecol.Lett., 11, 1294-1303.

Cortes-Avizanda, A., Almaraz, P., Carrete, M., Sanchez-Zapata, J. A., Delgado, A., Hiraldo, F. & Donazar, J. A. (2011). Spatial heterogeneity in resource distribution promotes facultative sociality in two trans-Saharan migratory birds. Plos One, 6, e21016.

Dempster, T., Sanchez-Jerez, P., Uglem, I. & Bjorn, P. -. (2010). Species-specific patterns of aggregation of wild fish around fish farms. Mar Ecol. Prog. Ser, 86, 271-275.

Dempster, T., Uglem, I., Sanchez-Jerez, P., Fernandez-Jover, D., Bayle-Sempere, J., Nilsen, R. & Bjorn, P. A. (2009). Coastal salmon farms attract large and persistent aggregations of wild fish: An ecosystem effect, Mar. Ecol. Prog. Ser., 385, 1-14.

Dempster, T., Fernandez-Jover, D., Sanchez-Jerez, P., Tuya, F., Bayle-Sempere, J., Boyra, A. & Haroun, R. (2005). Vertical variability of wild fish assemblages around sea-cage fish farms: Implications for management. Mar. Ecol. Prog. Ser., 304, 15-29.

Dempster, T., Sanchez-Jerez, P., Fernandez-Jover, D., Bayle-Sempere, J., Nilsen, R., Bjorn, P. & Uglem, I. (2011). Proxy measures of fitness suggest coastal fish farms can act as population sources and not ecological traps for wild gadoid fish. Plos One, 6, e15646.

Department of Fisheries and Aquaculture, Planning Services Division. Newfoundland and Labrador Fisheries and Aquaculture Annual Report: 2010-2011.

Fernandez-Jover, D., Sanchez-Jerez, P., Bayle-Sempere, J. T., Valle, C. & Dempster, T. (2008). Seasonal patterns and diets of wild fish assemblages associated with mediterranean coastal fish farms. ICES J.Mar.Sci., 65, 1153-1160.

Fernandez-Jover, D., Lopez Jimenez, J. A., Sanchez-Jerez, P., Bayle-Sempere, J., Casalduero, F. G., Martinez Lopez, F. J. & Dempster, T. (2007). Changes in body condition and fatty acid composition of wild Mediterranean horse mackerel (*trachurus mediterraneus, steindachner*, 1868) associated to sea cage fish farms. Mar.Environ.Res., 63, 1-18.

Fuller, R. & Glue, D. (1980). Sewage works as bird habitats in Britain. Biol.Conserv., 17, 165-181.

Grémillet, D., Pichégru, L., Kuntz, G., Woakes, A., Wilkinson, S. Crawford, R., & Ryan, P. (2008). A junk-food hypothesis for gannets feeding on fishery waste. Proc. Roy. Soc. B., 275, 1149-1156

Jolly, G. & Hampton, I. (1990). A stratified random transect design for acoustic surveys of fish stocks. Can.J.Fish.Aquat.Sci., 47, 1282-1291.

Katz, T., Herut, B., Genin, A. & Angel, D. (2002). Gray mullets ameliorate organically enriched sediments below a fish farm in the oligotrophic Gulf of Aquaba (red sea), 234, 205-214.

Levin, S. (1992). The problem of pattern and scale in ecology. Ecology, 73, 1943-1967.

Oakes, C. & Pondella, D.J. (2009). The value of a net-cage as a fish aggregating devince in Southern California. Journal of the World Aquaculture Society, 40, 1-21.

Park, K. J. & Cristinacce, A. (2006). Use of sewage treatment works as foraging sites by insectivorous bats. Anim.Conserv., 9, 259-268.

Robb, G. N., McDonald, R. A., Chamberlain, D. E. & Bearhop, S. (2008). Food for thought: Supplementary feeding as a driver of ecological change in avian populations. Front. Ecol. Environ., 6, 476-484.

Roth,Timothy C.,,II & Lima, S. L. (2007). Use of prey hotspots by an avian predator: Purposeful unpredictability? Am.Nat., 169, 264-273.

Rose, G.A. & Porter, D.R. (1996). Target-strength studies on Atlantic cod (Gadus morhua) in Newfoundland waters. ICES J. Mar. Sci., 53, 259-265.

Sih, A. (2005). Predator–prey space use as an emergent outcome of a behavioral response race. in P. Barbosa and I. Castellanos, editors. The ecology of predator–prey interactions. Oxford University Press, Oxford, UK.

Simmonds, E. & Fryer, R. (1996). Which are better, random or systematic acoustic surveys? A simulation using north sea herring as an example. ICES J.Mar.Sci., 53, 39-50.

Simmonds, J. & MacLennan, D.N. (2005). Fisheries Acoustics: Theory and Practice, Second Edition. Blackwell Science.

Tuya, F., Sanchez-Jerez, P., Dempster, T., Boyra, A. & Haroun, R. J. (2006). Changes in demersal wild fish aggregations beneath a sea-cage fish farm after the cessation of farming. J.Fish Biol., 69, 682-697.

Uglem, I., Dempster, T., Bjorn, P., Sanchez-Jerez, P. & Okland, F. (2009). High connectivity of salmon farms revealed by aggregation, residence and repeated movements of wild fish among farms. Mar. Ecol. Prog. Ser., 384, 251-260.

Valle, C., Bayle-Sempere, J. T., Dempster, T., Sanchez-Jerez, P. & Gimenez-Casalduero, F. (2007). Temporal variability of wild fish assemblages associated with a sea-cage fish farm in the south-western mediterranean sea. Estu. Coast. Shelf Sci., 72, 299-307.

Vita, R., Marin, A., Madrid, J., Jimenez-Brinquis, B., Cesar, A. & Marin-Guirao, L. (2004). Effects of wild fishes on waste exportation from a Mediterranean fish farm. Mar. Ecol. Prog. Ser., 277, 253-261.

Wiens, J. (1989). Spatial scaling in ecology. Funct. Ecol., 3, 385-397.

Yang, L. H., Bastow, J. L., Spence, K. O. & Wright, A. N. (2008). What can we learn from resource pulses? Ecology, 89, 621-634.

Yang, L. H., Edwards, K. F., Byrnes, J. E., Bastow, J. L., Wright, A. N. & Spence, K. O. (2010). A meta-analysis of resource pulse-consumer interactions. Ecol.Monogr., 80, 125-151.

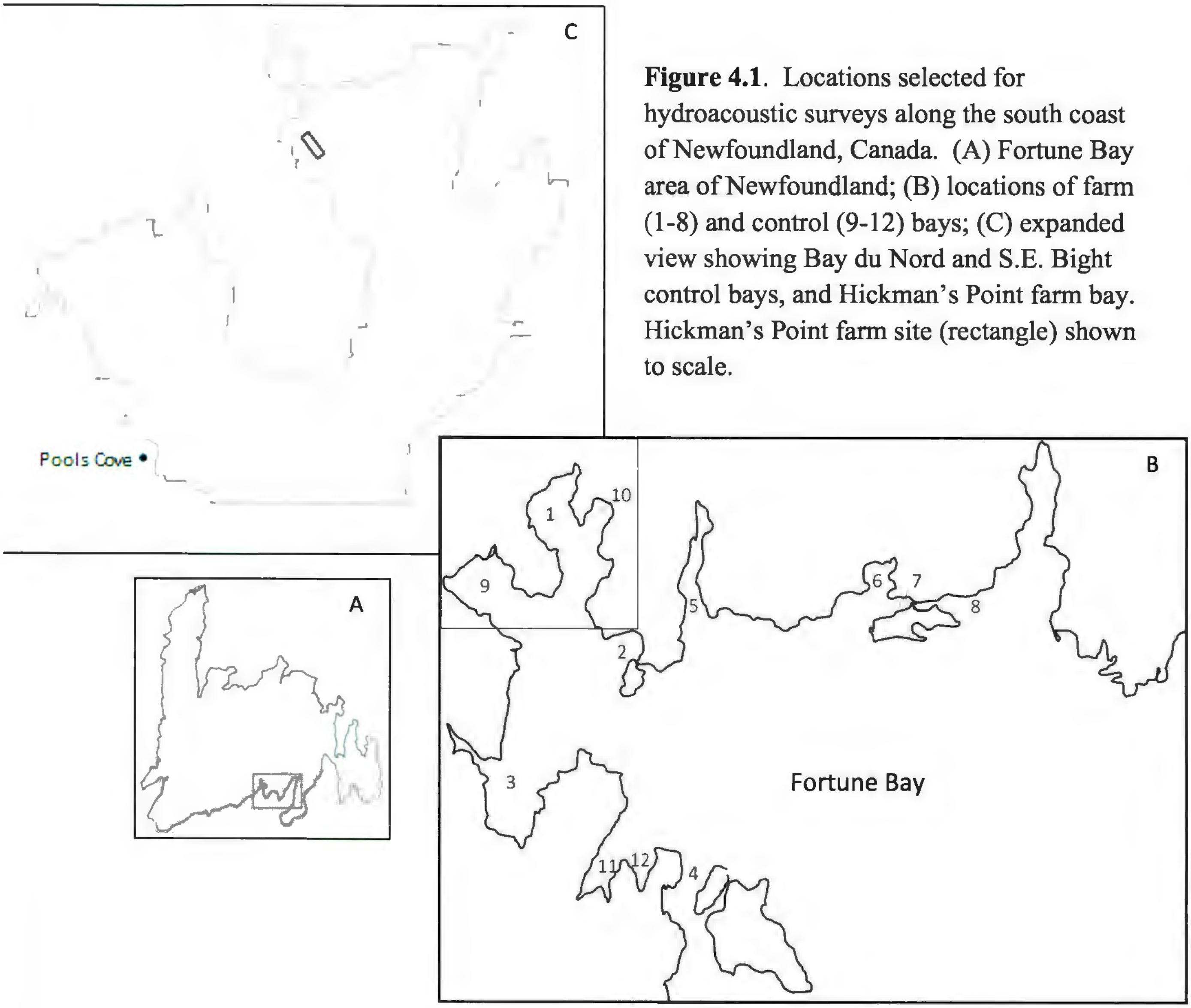

Figure 4.1. Locations selected for hydroacoustic surveys along the south coast of Newfoundland, Canada. (A) Fortune Bay area of Newfoundland; (B) locations of farm (1-8) and control (9-12) bays; (C) expanded view showing Bay du Nord and S.E. Bight control bays, and Hickman's Point farm bay. Hickman's Point farm site (rectangle) shown to scale.

Table 4.1. Characteristics of salmon farm and control bays in the Fortune Bay region of Newfoundland. With the exception of Bay du Nord, control bays are locations that have no history of aquaculture, but that have been leased for future salmon operations by the aquaculture industry. Bay du Nord previously supported 1 salmon farm but has been in fallow for 3 years.

	Site Number	Site	Area (m^2)	Depth (m)	No. Transects	No. Cages
Farm	1	Hickman's Point	4.7	60	6	8
	2	McGrath's C South	1.8	50	3	12
	3	Cinq Isle/Tilt Cove	12.5	60	9	26
	4	Ironskull Point	3.3	70	6	18
	5	Old Woman's Cove	2.1	65	6	14
	6	Deep Water Point	1.8	80	3	14
	7	Little Burdock Cove	1.0	60	3	12
	8	Rencontre Island	1.3	50	3	16
Control	9	Bay du Nord	7.5	50	9	0
	10	South East Bight	1.5	50	3	0
	11	Corbin Bay	5.4	60	6	0
	12	Hatcher Arm	2.4	70	3	0
	13	Doctors Harbour	0.5	80	1	0

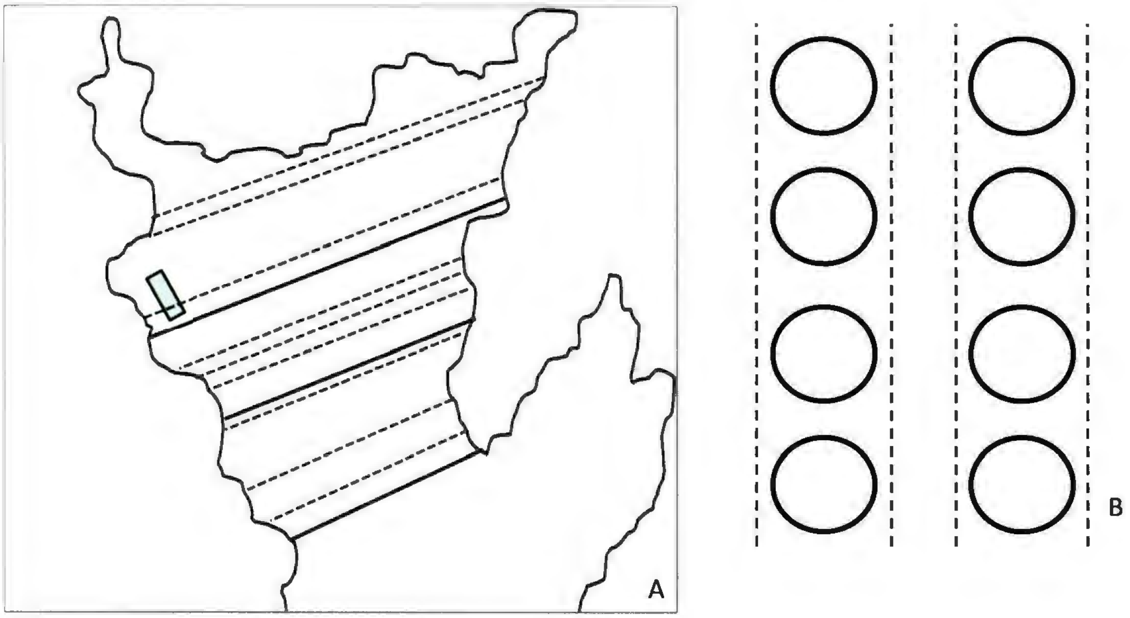

Figure 4.2. Illustration of hydroacoustic survey design used to assess distribution of marine life in a farm bay and at a farm site (grey square); (A) stratified randomized sampling of farm bay, showing 3 systematic strata (solid lines). Each 1 kilometer long strata was divided into a hundred 10 meter segments, 3 of which were randomly chosen as survey transects (stippled lines); (B) linear transects used to survey wild fish aggregations below and immediately adjacent to sea cages within one farm site. Illustrated is a farm site composed of 2 parallel rows of 4 sea cages (circles). Each sea cage is approximately 10 meters in diameter and 20 meters deep. Hydroacoustic transects (stippled lines) were surveyed approximately 5 meters from sea cages.

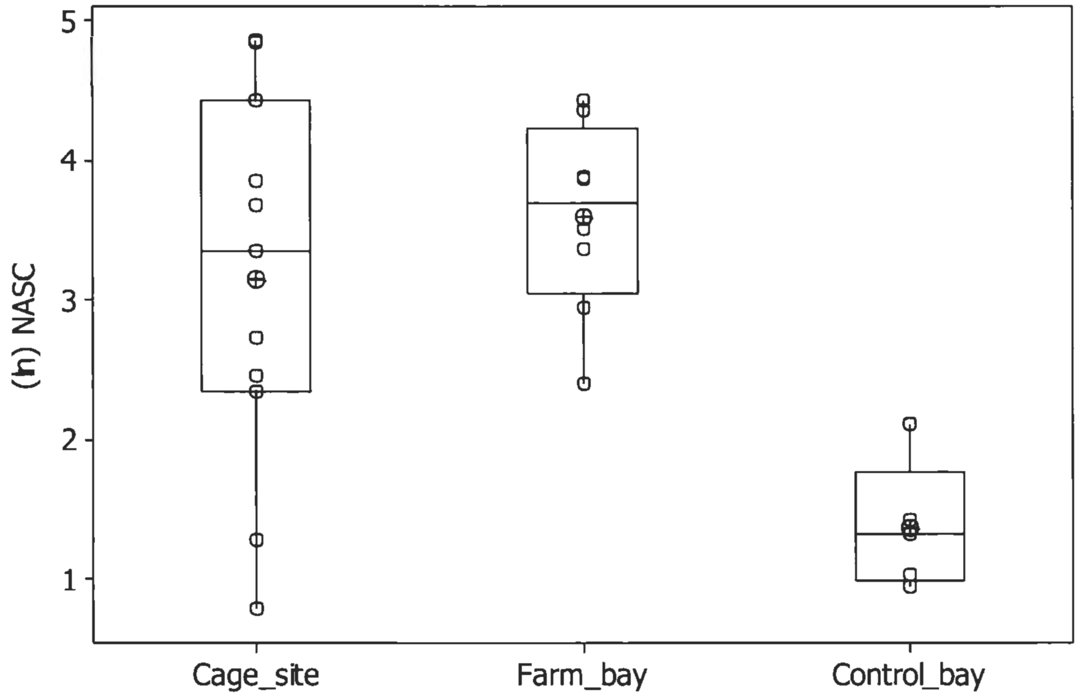

Figure 4.3. Mean biological activity, measured by nautical area backscatter coefficient (NASC) is greater in bays that contain salmon farms (n= 8 bays) and adjacent to sea cages (n=11) compared to control bays (n= 5 bays). With the exception of one bay that supported aquaculture 3 years prior to my study, control bays have no history of salmon farming but have applied for future use by the industry. Box plot shows median and interquartile range. Crossed circles show mean. Box and whiskers show 10th and 90th percentiles, respectively.

Chapter 5. General conclusions

As we continue to develop and industrialize natural land- and seascapes, we must be cognisant of how environmental change affects the distribution, abundance, and behaviours of wild organisms. One aspect of change that has not been previously considered is how environmental change that acts to reduce variability in naturally fluctuating biological and physical resources may affect animals that have adapted to cope or exploit this variability. The introduction of predictable resource patches into the environment is widespread, and the sum of these introductions may be the creation of a patchy landscape in which the distribution of resources is highly predictable through space and time.

In Chapter 2, I develop a framework for understanding the effects of resource predictability on animals, using examples from the foraging literature. My treatment of information as a commodity thats value is scale-dependent is a novel contribution to the field of information ecology and to foraging theory. I also use this chapter to provide future direction for the study of predictability, highlighting the need for experimental studies that address the value of predictability to foraging animals, and that explore these effects in the field.

In Chapter 3, I use the Ideal Free Distribution theory to determine the value of resource predictability in a laboratory experiment. My results demonstrate that there is a net benefit to foraging where resources have become temporally predictable, and that the preference for resource predictability results from energetic savings on information. This experiment is a simple and effective demonstration of the effects of resource predictability on animals that use information to make foraging decisions, and provides the incentive for further exploration of this effect in the field.

In Chapter 4 I begin to explore the effects of introducing novel and highly predictable resource patches into natural environments. Since patterns of resource availability in coastal marine environments tend to be unpredictable, the introduction of sea cages, where food distributions are highly predictable through space and time, should have a profound effect on animals that have adapted to a high degree of variability. Using the large-scale distribution of animals as an indicator of perceived habitat quality, my results confirm that sea cage sites are preferential foraging locations; however, I am unable to distinguish the effects of predictability from the more general effects of introducing a quantity of food into the environment.

The most significant contribution of the research herein is the theoretical development of the study of resource predictability. Although I begin to test and quantify the effects of predictability in an experimental and field population, I do not imply that my research provides conclusive evidence to support my theory. My hope is that this research will provide a strong foundation for the study of predictability and incentive for future pursuits in this field.

Appendix

Appendix I. Settings for the echosounder (Simrad EK500) with 38 kHz, split beam transducer (ES38B) during the September 2011 surveys.

Transducer depth (m)	1
Absorbtions coefficient (dB km -1)	0.01
Pulse length (ms)	medium=2
Bandwidth (kHz)	auto
Maximum power (W)	2000
Two-way beam angle (dB)	-20.6
Sv transducer gain (dB)	25.9
Angle sensitivity alongship	21.9
Angle sensitivity athwartship	21.9
3 dB beam width alongship (^{0})	7.15
3 dB beam width athwartship(^{0})	7.08
Alongship offset (^{0})	-0.03
Athwartship offset (^{0})	-0.07
Bottom minimum threshold (dB)	-48
TS minimum (dB)	-70