PREDATION-RISK IN JUVENILE ATLANTIC COD WITH RESPECT TO EELGRASS PATCH CHARACTERISTICS IN NEWMAN SOUND, BONAVISTA BAY, NEWFOUNDLAND

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Predation-risk in juvenile Atlantic cod with respect to eelgrass patch characteristics in Newman Sound, Bonavista Bay, Newfoundland

by

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A thesis submitted to the
School of Graduate Studies
in partial fulfillment of the
requirements for the degree of
Master of Science

Department of Biology
Memorial University of Newfoundland

August 2004

St. John's Newfoundland

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395, rue Wellington
Ottawa ON K1A 0N4
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Your file Votre référence
ISBN: 0-494-02342-2
Our file Notre référence
ISBN: 0-494-02342-2

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ABSTRACT

Predation risk is a driving force in the distribution of juvenile fish. In coastal Newfoundland, age-0 Atlantic cod (*Gadus morhua*) use the protective cover of eelgrass (*Zostera marina*) in preference to exposed, sandy areas. Studies suggest that habitat configuration is closely correlated to the population dynamics of certain species. A relationship between eelgrass patch morphology and predation risk of cod could allow for indirect assessment of natural predation based primarily on eelgrass configuration – a variable more easily quantified than natural predation itself. In three experiments, I used a tethering technique in Newman Sound, Bonavista Bay, Newfoundland, Canada, to quantify the relative predation risk of post-settled age-0 cod in natural eelgrass habitats. I examined the influence of eelgrass patch size (1-80 m^2) on predation risk based on the assumption that larger patch size results in lower predation compared to small patches. I also tested for the presence of edge effects at an 18 m long, vertical boundary between a mud and an eelgrass habitat. Lastly, I evaluated the effect of patch shape on predation by quantifying the fractal exponent of individual patches. I conclude that predation was correlated to patch area and proximity to patch edge, but not to the shape of individual patches.

ACKNOWLEDGEMENTS

I accredit the completion of this thesis to the invaluable guidance and assistance of the following:

Dr. David Schneider, my supervisor, for conversations about the nervous system, railroad cars, and those negative Hessians. I finally figured out how all of these apply to cod.

I offer my sincerest gratitude to my co-supervisor, Dr. Robert Gregory, for his utmost patience and support in the field and in the office.

Sincere thanks to my additional committee members, Dr. Joe Brown and Dr. Joe Wroblewski, as well as Dr. Ben Laurel, Dr. David Methven, Danny Ings and Dr. Dave Robichaud for their considerable intellectual contributions. Danny Ings and Trevor Avery provided me with aid in a painful process called 'data analysis'. Thank you so much.

I would not have been able to conduct such extensive fieldwork without the technical assistance and emotional support of Miriam O, Phil Sargent, Nadine Wells, Janelle Hancock, Christina Anderson, Jessica Anderson, Scott Moulton, Peter Frampton, Gregory Sparkes, Doug Gibson, Dave Cote, Adam Ogilvie, Terralynn Landers, and Dan Porter.

I am ever-grateful to JP and my family for trusting that I would return to the Midwestern U.S. after having experienced such an amazing place as Newfoundland.

Lastly, I am truly appreciative for the financial support for this study provided by NSERC, Terra Nova National Park (Parks Canada) and the Canadian Department of Fisheries and Oceans.

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LIST OF ABBREVIATIONS

A – Area

ABS – Acrylonitrile-Butadiene-Styrene

β_x – Change in Risk due to the Factor or Interaction (x)

D_e – Depth

D_i – Distance

E1, E2 – Study sites for the Edge Effects Experiment

EFH – Essential Fish Habitat

f_e – Expected Frequency

f_o – Observed Frequency

G – Goodness of Fit

L – Sampling Location

OR – Odds Ratio

P – Sample Period

P: A – Perimeter to Area Ratio

P1-P3 – Study sites for the Patch-Size Experiment

p_I – Proportion of Tether Sets where Predation was Observed

p_0 – Proportion of Sets with Predation for the Reference Class

q_0 – Proportion of Sets without Predation for the Reference Class

q_I, – Proportion of Sets without Predation

S – Site

SL – Standard Length

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Chapter One – Introduction

In conjunction with anthropogenic disturbance and exploitation, the inability to accurately assess the number of individuals in a population is a primary factor in the decline of commercially-harvested as well as non-commercial species worldwide. Standard single-species population models relied heavily on fine-scale field collections, including visual surveys and mark-recapture assessments, of individuals at various life stages combined with estimates mortality. Some models consider natural mortality to be negligible to fishing-related mortality. However, predation is a greater source of mortality for certain species in certain areas (Sissenwine et al. 1984, Tsou and Collie 2001), especially for younger individuals within a population (Bax 1998). Early models also had little regard for factors that change across a variety of spatio-temporal scales (e.g. daily or seasonal changes in migration, foraging or predation) for each life stage, which contributed to the inaccuracy of estimates when scaling models up in space and time.

To improve population assessments, some management plans, such as the Northeast Multispecies Fish Management Plan (established in 1986 by the New England Fisheries Management Council) and Multi-Species Virtual Population Analysis (MSVPA) (established in 1991 by the International Council of the Exploitation of the Sea), use a multi-species approach to examine the combined effects of species interactions and fishing mortality on populations. One difficulty with such models is that they rely primarily on accurate calculations of predation mortality. In the MSVPA model, predation morality is calculated as a function of the consumption rate of a predator (by species, by age), which is determined by stomach-content data, and the proportion of species and age-specific availability of suitable prey, which is determined by catch-at-age data (Tsou and Collie 2001). This model requires an extensive amount of data and assumes that information that is gathered from these surveys can be extrapolated to areas where these surveys were not conducted. This assumption is not always correct, especially when catch data is taken from Commercial Landings. Commercial fishing inevitably occurs where catches are the greatest, i.e. there are fish (predator and prey) aggregations, and is not representative of areas with lower densities. As in the case of Atlantic cod adults that aggregate to spawn, this can lead to overestimates of individuals. Another problem with this model is that is that it ignores the fact that predatory success varies depending on the local habitat. Although they are an improvement over single-species models, multi-species models may still not provide the best population estimates.

More recently, Delong and Collie (2004) model fish abundance in the Northwest Atlantic as a function of habitat variables (e.g. sediment, temperature) and geographic location through the identification of Essential Fish Habitat (EFH). One flaw in this model is that abundance is estimated independent of actual fish data. This model assumes that fish abundances and survival are equivalent in all EFH areas. To improve ecosystem-based models such as the one proposed by Delong and Collie (2004), it is imperative to understand variable survival in or preference for essential habitats, which may be a function of various physical characteristics of these preferred environs.

Due to the vast distribution of fish home ranges across life stages and the extensive data collection necessary to generate reasonable population models, it would be beneficial to integrate an indirect method for assessing predation mortality into current multi-species and ecosystem-based models. In recent years, research in landscape ecology has demonstrated a correlation between population dynamics and preferred habitat. Studies noted not only a presence-absence relationship but also correlations between dynamics and patch size (Hobbs 1988, Sovada et al. 2000) or landscape configuration (Stamps et. al 1987, Andren and Angelstam 1988, Donovan et al. 1997, Moen and Jonsson 2003). Although recent efforts have been made in aquatic habitats (Irlandi 1997, Eggleston et al. 1998, Laurel et al. 2003), such research has been predominantly conducted in terrestrial environments. The bias towards terrestrial research is primarily attributed to the difficulty of conducting underwater measurements as opposed to those on land. To facilitate the quantification of underwater habitat configuration, aquatic studies have primarily used artificial vegetation, which can be constructed to be relatively homogeneous and to fit a desired configuration and can be measured on land prior to deployment. To date, no efforts have successfully demonstrated the relationship between population dynamics and naturally-occurring vegetation patterns in aquatic systems.

There are a variety of techniques that have been implemented to quantify habitat area and configuration. Many of these initial attempts at quantifying aquatic habitat have consisted of simple in-field measurements (e.g. measuring tape) at very fine-scales. As broad-scale data such as Landsat satellite imagery are becoming more readily available, it may be possible to conduct these fine-scale habitat assessments regionally. The multi-spectral color bands of remotely-sensed data can be digitally-analyzed in a Geographical Information System (GIS) and vegetation categories can be validated using minimal ground-truthing in the field. Because data such as Landsat 7 imagery are taken on a monthly basis, it is possible to look at changes in habitat area and configuration over time. Currently, the limitation of such readily-available data is the resolution at which it is collected. Landsat 7 imagery has a $28m^2$ pixel size, which may be too coarse for assessing individual patch characteristics for some types of habitats. Although aerial photography can be taken at sub-meter pixel sizes, this data is not available for all regions. It is likely that Landsat resolution will improve and aerial photography will become more geographically available in the near future. Until then, in-field measurement is the most common technique for fine-scale habitat analysis.

The status of the Atlantic cod (*Gadus morhua*) population in the Northwest Atlantic is a prime example of inaccurate population assessment and, in turn, management. The inability to accurately assess (and manage) cod stocks resulted in the 1992 fishing moratorium in the northwest Atlantic and the International Council for Exploration of the Sea's current advisory of zero fishing pressure (International Council for the Exploration of the Sea 2003). Prior to the moratorium, recruitment models focused on knowledge of older individuals and their spawning potential. More recent research documents the necessity of understanding early juvenile stages of Atlantic cod (*Gadus morhua*) in order to quantify recruitment to the fishery (Sissenwine et al. 1984, Campana et al. 1989, Asthorsson et al. 1994, Anderson and Dalley 1997, Helle et al. 2000).

Evidence suggests that that mortality of young fish is primarily attributed to predation (Swain and Sinclair 2001). As post-settled individuals, predator-response mechanisms are varied in young cod, and include the use of structurally complex habitats as refugia. In particular, individuals in coastal environments may seek refuge in nearshore eelgrass (*Zostera marina*) beds, which are often comprised of mosaics of patches, fragmented by storms and ice-scouring. Based on the information provided by the aforementioned research in landscape ecology, predators (as well as the young cod themselves) may respond differentially within complex eelgrass habitats. That is, the spatial configuration of patches may affect predation risk and, within patches, predation may be elevated near the edge.

Such information could be valuable in the integration of the habitat component into modern recruitment models. Without this knowledge, the (incorrect) assumption would be that fish abundance could be calculated from the areal extent of eelgrass available in addition to the existing model components (e.g. fecundity, natural mortality). Evidence showing varied predation potential within these habitats would allow for a more accurate assessment of the population based on the spatial configuration of the available habitat.

Although eelgrass has been shown to reduce the risk of predation of young cod, it has not yet been determined if the geometry of individuals patches may affect predation rates. The objective of this thesis is to quantify the relative predation risk of post-settled age-0 Atlantic cod in eelgrass habitats with respect to the physical parameters of individual eelgrass patches. Chapter 2 consists of a literature review that establishes the role that predators exhibit with respect to the spatial distribution of young cod from egg to post-settlement. Based on the assumption that more eelgrass should provide more refuge, thus lowering the risk of predation, I examine the relationship between the areal extent of patch coverage and predation risk in Chapter 3. Additionally in Chapter 3, I assess whether or not predators respond to edge effects in eelgrass habitats. Because of the results obtained from the patch-size and edge effects experiment, I also examined the role of patch shape (i.e. the amount of edge per unit area) in relation to predation risk in Chapter 4. The results of this thesis illustrate the importance of eelgrass morphology with respect to predator-related mortality of young cod as well as the spatial scales across which this relationship is maintained.

Chapter Two - A Literature Review regarding the distribution of young juvenile cod as a response to predator distribution

2.1 Background

Previous efforts to understand the spatio-temporal distribution of commercial fish species often focused on large-scale explanations such as oceanographic factors or physiological limits. Management of the Atlantic cod fishery, in particular, primarily focused on numbers of spawning individuals and potential egg production and large-scale processes that may affect fish at these stages (e.g. hydrographics). One likely source of the recent interest in early juvenile stages is research demonstrating that survival of post-larval and juvenile fish is a better predictor of year-class strength than survival of eggs and larvae (Campana et al. 1989). Although current management strategies focus on large-scale explanations for the distribution of the earliest juvenile stages, recent research on individual behavior demonstrates that young fish are capable of assessing their surroundings and behaving in such a way that can maximize their fitness. By demonstrating that young fish are acting in response to meso-scale factors, it becomes apparent that models based on large-scale processes may be too broad and individual-based models need to be considered.

Despite the fact that Swain and Sinclair (2000) primarily attribute poor recruitment of early-stage individuals to predation, there has been little attention given to the influence that predators have over the meso-scale distribution of young cod. Work conducted at larger scales demonstrates a distribution overlap of small and large conspecifics within nurseries during their early juvenile years (0-3 years) resulting in high rates of cannibalism (Bogstad et al. 1994), although inter-specific predation is also influential at all stages (Hunter 1984, Oiestad et al. 1985, Tupper and Boutilier 1995b). At these scales, it is apparent that settling cod cannot avoid areas of high predator densities. At smaller scales, it is evident that young cod can assess local predation risk and make decisions based on these assessments (Gotceitas and Brown 1993, Gotceitas et al. 1995, Tupper and Boutilier 1995a, b, Fraser et al. 1996, Gotceitas et al. 1997). In this chapter, I discuss the factors affecting the distribution of cod from pelagic to post-settled juveniles. In particular, I review the influence that predators have on the distribution of coastal, demersal juveniles at various spatial and temporal scales, and the behaviors exhibited by young cod in response to the threat of predation.

2.2 Pelagic Eggs and Larvae

Atlantic cod are found in coastal and offshore shelf areas throughout the North Atlantic Ocean from southern Greenland and southeastern Baffin Island south to Cape Hatteras in the western Atlantic (Scott and Scott 1988) and the Barents Sea to the Bay of Biscay in the eastern Atlantic (Office of Seafood and Office of Regulatory Affairs 1993-2004). During the egg and early larval stage, individuals are advected by currents from spawning grounds towards nursery grounds. The advective processes that result in high concentrations of eggs and larvae also aggregate their prey. The success of planktonic larvae often relies on these passive processes, which retain them in a suitable habitat for future growth (Sinclair 1988), displace them from spawning to nursery grounds (Harden-Jones 1968) or enhance contact rates with prey, thus minimizing risk of starvation

(Werner et al. 1996, Leising and Franks 1999). Although passive processes are important to survival of eggs and larvae, these processes are highly variable and the distribution of spawning adults as well as the availability of suitable settlement habitat combined with transport mechanisms provide explanations for distribution (Pepin and Helbig 1997).

Considering the low escape response of larval fish, the influence of predatory forces on the distribution of larval cod should not be overlooked (Bottcher et al. 1998). Larval cod survival is highly sensitive to fish and invertebrate predators, such as large crustaceans and jellyfish (Hunter 1984, Oiestad et al. 1985), and these fish fare well in habitats absent of predators (Oiestad et al. 1985). Eggs are also highly susceptible to predation. Hunter (1984) attributes up to 98% of mortality to predator consumption. As opportunists, larval cod can thrive in both nutritionally-poor and nutritionally-rich environments (Garrison et al. 2000). In areas of great prey densities, larval fish tend to grow longer (Williams et al. 1996) and those with a higher condition index have notably better escape responses (Elliott and Leggett 1998). However, compared to larval haddock, larval cod can also survive in nutritionally-poor areas, which are likely to have fewer predators, thus giving them the ability to avoid areas of high predation potential (Garrison et al. 2000). Therefore, larvae exposed to either nutritionally-poor or nutritionally-rich habitats both have means of alleviating predation.

2.3 Pelagic Juveniles

At ~ 12 mm, metamorphosis from the larval to the juvenile stage begins (Pedersen et al. 1989). This transition typically includes changes in digestion (Pedersen and Falk-Petersen 1992) and external appearance (Balon 1975) in addition to coincident changes in behavior, including locomotion and foraging tactics (Balon 1975). By ~20-40 mm (Bolz and Lough 1988, Bottcher et al. 1998), juvenile cod are considered pelagic juveniles, feeding on small zooplankton such as calanoid copepods and mysid shrimp (Perry and Neilson 1988).

By examining the spatio-temporal distribution of individuals as they gain control over locomotion, we can indirectly assess the effects of predators (and prey) by the use of habitats by various year classes (Anderson and Gregory 1999). Even though finding food and avoiding becoming food are the primary 'concerns' of most individuals, there is some geographic variability in behaviors. Inter-annually, distribution of pelagic juveniles off the Icelandic coast was 3-4 times greater in shallow areas (<50m deep) compared to deeper areas (51-200 m) and corresponded with zooplankton density (Asthorsson et al. 1994). Greater prey biomass is attributed to higher survival rates, but not greater average length, at earlier stages. On the other hand, Suthers et al. (1989) compared growth and abundance of inshore and offshore populations of postlarval cod in southwestern Nova Scotia to zooplankton biomass. The authors found higher prey densities and growth rates in the offshore, which were negatively correlated with postlarval cod abundance. This suggests that pelagic juvenile cod may not select the nearshore simply for food purposes.

Upon examination of diel patterns, offshore individuals in Iceland tended to remain higher in the water column during the day (Godo et al. 1989, Bottcher et al. 1998) than their Georges Bank counterparts, which were at the bottom early in the day and reached midwater by evening (Perry and Neilson 1988). Perry and Neilson (1988) note that these migrations on Georges Bank may be a means of alleviating interspecific competition with larval haddock. The authors found more distinct migrations of cod when prey densities were low and less vertical distinction between cod and haddock in areas of greater prey availability. In the eastern Baltic, pre-settled fish retreated to the bottom at night (Bottcher et al. 1998). Because these fish were not yet feeding on epibenthos, one explanation for this demersal activity may be that they are searching for suitable habitat in which to settle. By searching at night, they are also able to avert the risk of predation (Linehan et al. 2001).

2.4 Settling Juveniles

Settling juveniles are individuals undergoing the transition from the pelagic to demersal stage. Overall, settlement can occur at a size of 25-80 mm in cod, although there is a considerable degree of geographic variability: 25-40 mm (R.S. Gregory, unpublished data, 2000 [coastal Newfoundland]), ~30-60 mm (Tupper and Boutilier, 1995a [Nova Scotia]), 50-60 mm (Robb and Hislop 1980 [North Sea]), ~50 mm (Hussey et al. 1997 [Baltic]), 30-50mm settle (Bjornstad et al. 1999 [Norwegian Skagerrak Coast]), 40-70 mm (Bottcher et al. 1998 [eastern Baltic]), 60-80 mm (Bolz and Lough 1988 [Georges

Bank]), 38-65 mm (Grant and Brown1998a) [coastal Newfoundland]). The literature offers several explanations not only for the variability in minimum and maximum sizes, but also the extent of the size range over which settlement is occurring.

One fundamental issue is the debate over the definition of 'settlement'. Bowman (1981) describes settlement in cod as the point at which >50% of prey items are benthic. Recent evidence suggests that this definition may be inadequate. Hussey et al. (1997) and Lomond et al. (1998) have found that post-settled age-0 cod in both coastal and offshore locations may continue to feed on pelagic prey after the vertical transition to a benthic existence has clearly been achieved. This evidence suggests that the definition of settlement in cod must include an individual's spatial distribution as well as its dietary make-up (which can be a function of prey availability).

Because of the issue with the definition of settlement, there is debate over whether this is a gradual or abrupt process. Reasons supporting that this is a rapid shift include the fact that they start feeding demersally as soon as they reach a gape-size large enough to handle benthic prey (Lomond et al. 1998) and that the 14 day transition (in the Baltic Sea) is short relative to other species (Hussey et al. 1997). Conversely, most authors have described settlement in cod as a gradual metamorphosis (Bowman 1981, Bolz and Lough 1988, Pedersen and Falk-Petersen 1992, Benoit et al. 2000). Support for a gradual transition includes the fact that otoliths do not have apparent markings associated with settlement that would indicate elevated levels of physiological stress (Bolz and Lough

1988) and that cod undergo slow physiological development of the stomach and pyloric caeca compared to other species (Pedersen and Falk-Petersen 1992). Lastly, the fact that fish that have clearly achieved settlement still feed on pelagic prey is also an indication that settlement is gradual. It is possible that cod transform physiologically more slowly than they do behaviorally. It is also likely that subtle changes in behavior are simply difficult to note, thus making the behavioral transition seem more abrupt.

By studying the length of time that it takes to settle, inferences can be made about the environmental assessment capabilities of fish at this stage as well as the availability of suitable settlement habitat. As we explore some of the behaviors associated with the settlement process, it becomes clear that the transition may be variable due to environmental factors. Ideally, one would expect these individuals to undergo a rapid transition from the open pelagia to the more structurally complex refugia of the benthos as a predator-avoidance mechanism (Lomond et al. 1998). That is, considering their new cryptic coloration, they should be attempting to minimize mortality while maximizing growth (Werner and Gilliam 1984) by moving to the bottom, where they could hide from predators amongst the substratum and feed solely on benthic prey items. The fact that settlement, according to the behavioral definition, occurs at larger sizes or over a broader size range in some locations suggests that these fish may be stalling for some reason - a behavior that other species of settling fish have demonstrated (Robertson et al. 1999 [Pomacentrids], Victor 1986a [Labrids], Cowen 1991 [wrasses]).

As Benoit et al. (2000) states, “Timing is not a haphazard process”. Modeling performed by Salvanes et al. (1994) combined with empirical data collected by Godo et al. (1989) demonstrates that cod in western Norway are actually undergoing this habitat shift when the mortality to growth rate ratio is greatest. In other species that undergo settlement at sizes similar to cod, there is evidence for small-scale habitat preferences (Modin and Pihl 1996 [recently settled plaice and flounder]), predator recognition, avoidance and escape (Wennhage and Gibson 1998 [settling plaice]), nocturnal settlement in areas of visual, diurnal predators (Leis 1991, Victor 1991 [coral reef larvae]) and even pre-settlement schooling (Leis & Carson-Ewart 1998 [coral reef larvae]). Such behaviors are often responses to chemical cues from resident fish (Sweatman 1988), vegetation (Carr 1994), and food composition (Levin 1994) to determine where and when it will settle (Wennhage and Gibson 1998). The variation in and complexity of these behaviors suggests that late larval fish are not passive creatures (Leis & Carson-Ewart 1998) and act in response to their environment.

There is also ample evidence that lack of suitable substrate can be a reason for variability in the timing of settlement (Marliave 1977, Jackson and Strathmann 1981, Victor 1986). Atlantic cod settle in either inshore coastal waters or on offshore shoals. Densities of settling fish are highest in shallow, inshore nurseries (e.g. Dalley and Anderson 1997 [coastal Newfoundland], Hawkins et al. 1985 [Loch Torridon, Scotland]) that may maximize growth and survival by providing food and shelter. Shallow regions may be preferable for settlement, because these areas facilitate bottom-habitat sampling during the pelagic to demersal transition. Because the vertical migration distance to the bottom is shorter in shallow water, semi-pelagic individuals can continue to forage from the water column until the benthic transition is completed. The notion that inhabiting shallow, nearshore waters may facilitate settlement is supported by the suggestion that inshore individuals may settle earlier than their offshore counterparts (Anderson and Dalley 1997, Dalley and Anderson 1997, Methven and Schneider 1998). To avoid predators, offshore individuals tend to feed diurnally and sample benthic environments at night (Bottcher et al. 1998) when predation potential is low (Linehan et al. 2001), whereas settling cod in nearshore nurseries seek out areas of greater structural complexity (Tupper and Boutilier 1995a), which are known to reduce predator efficiency (Glass 1971, Cooper and Crowder 1979, Werner et al. 1983, Mattila 1992, Tupper and Boutilier 1995b). These behaviors indicate that cod may exhibit a wide range of settlement sizes because the quantity or spatial location of resources (i.e. vegetation, suitable habitat) or threat of predation is geographically variable.

2.5 Post-settled age-0 juveniles

Once individuals fully settle into benthic habitats, they are considered ‘post-settled’. Recently settled cod (38-65 mm) have a “barred or checkerboard pigmentation on a pale background” with a “silvery underside” (Grant and Brown 1998b). As they grow within their first year, they can reach sizes range from 50-130 mm (Lough et al. 1989 [Georges Bank]) to 70-160 mm (Hussey et al. 1997 [Baltic Sea]). By the time they reach 50-70 mm, they become mottled and heavily pigmented with a white underbelly (Grant and

Brown 1998b). This cryptic coloration may be an especially important defense against predation in their new, demersal habitats

Post-settled cod are characterized as opportunistic foragers and utilize the most abundant food resource available (Lough et al. 1989). Small (~ < 4mm) crustacean zooplankton, such as copepods and amphipods, are common prey items (Grant and Brown 1998b, Lomond et al. 1998), but gastropods and bivalves are also consumed (Hop et al. 1994). In coastal Newfoundland, the condition of age-0 cod remained well above the level of critical condition at which fish died in the laboratory, and fish did not even approach a critical point despite seasonal variation in size, abundance or prey availability (Grant and Brown 1999). This suggests that food is not a limiting resource in this study area. It is interesting to note that cod in this area settle at some of the smallest sizes recorded (25, 38 mm) (R.S. Gregory, unpublished data, 2000, Grant and Brown 1998b, respectively), again contributing to the idea that inhabiting shallower waters may reduce settlement time and that settlement may be rapid in areas where resources are not limiting.

Evidence suggests that extremely low survivorship in post-settled juveniles may be due to predation. Primary predators include larger gadids, including conspecifics (Bogstad et al. 1994, Salvanes et al. 1994, Grant and Brown 1998b, Linehan et al. 2001), as well as cunners (Linehan et al. 2001), and sculpin (Tupper and Boutilier 1995b, Linehan et al. 2001). At larger scales, the distribution trends of the youngest age classes is the same as with most species - depth of inhabitance tends to increase with age (or size) (Dalley and

Anderson 1997). One model estimates that the density of wild juveniles is only 40% of carrying capacity and that cannibalism (and food availability) should not limit production (Salvanes et al. 1992). However, at smaller scales, density-dependent processes are most likely between post-settled age-0's and age 1's, which have the greatest degree of spatial overlap (Bjornstad et al. 1999). In resource-limiting environments, intraspecific competition among cod is actually quite high (Bogstad et al. 1994) because of the overlap of food resource utilization across sizes (Hussey et al. 1997).

Because inshore and offshore settlement habitats differ physically and biologically, post-settlement dynamics can also differ greatly between habitats (Schneider et al. 1997). For this reason, I have divided the following sections into behaviors exhibited by inshore and offshore populations. Because the behavioral literature is biased towards shallow populations due to the logistics of sampling small fish in vast offshore areas (Bottcher et al. 1998), the section on inshore individuals is considerably more extensive.

2.5.1 Inshore populations

The degree of inter- and intra-annual site fidelity to a given location often reflects the food and refuge profitability of that area. Recently settled cod in the inshore remain in shallow nurseries for (most of) the duration of the year (Bjornstad et al. 1999). Within these nurseries, cod remain relatively localized within a few hundred meters in any habitat (Grant and Brown, 1998b). Tupper and Boutilier (1995a) found post-settled cod to be aggressive, territorial and site attached ($<50m^2$), whereas others found relatively high dispersal rates from a sample site (Hancock 2000). These discrepancies may be attributed to density-dependent site fidelity, due to limiting preferential habitat (Grant and Brown 1998b) and/or variability in prey abundance.

There is some debate in the literature over what occurs in coastal populations during the winter months. Inferences must be made, because sampling in ice-covered, nearshore waters is difficult to impossible, and fish this size could not be tagged electronically until recently. According to Asthorsson et al. (1994) and Anderson and Gregory (1999), it is unlikely that age-0's migrate in their first winter. However, they are capable of occupying deeper waters seasonally. Based on work in Trinity Bay, Newfoundland (Grant and Brown 1998b) and Loch Torridon, Scotland, (Hawkins et al. 1985), there is evidence that juveniles may overwinter in areas of settlement. Due to greater antifreeze capabilities, remaining in colder, shallow waters is more feasible for young cod than for adults (Kao and Fletcher 1988, Goddard et al. 1992), thus eliminating some level of predation. Other studies suggest that there is an offshore migration into warmer, deeper waters for the winter months (Macdonald et al. 1984, Methven and Bajdik 1994, Tupper and Boutilier 1995a, Gregory and Anderson 1997), indicated by a decrease in abundance during winter sampling and depth strata occupied. Until recently, the extent to which these fish are moving offshore has been difficult to assess. Recent developments in the radio tagging of small fish will make such research possible.

The importance of inshore nurseries for the survival of young cod is now well-established (e.g. Asthorsson et al. 1994, Hussey et al. 1997). Densities of demersal 0-group cod tend to be highest in waters less than 50 m deep (Godo et al. 1989 [Norway], Suthers and Frank 1989 [Nova Scotia], Asthorsson et al. 1994 [Iceland,), and decrease with depth (Asthorsson et al. 1994). Cod settling in the inshore environment are often found in shallow waters, less than 10 m deep (Riley and Parnell 1984) and may exhibit highest density at 4 - 7 m bottom depths (Methven and Schneider 1998).

Within the nearshore, young cod often associate with structurally complex aquatic landscapes. Norwegian age-0 cod, for example, are abundant in sheltered to semi-exposed areas (Godo et al. 1989) and are absent from extremely exposed areas 20-120 m deep (Godo et al. 1989, Fromentin et al. 1997). Preference by cod for eelgrass (*Zostera marina*) and other macroalgal habitats (e.g. *Desmarestia*, *Fucus*) compared to sand has been shown throughout their range (e.g. Tveite 1984 [Norway], Stottrup et al. 1994 [Denmark], Borg et al. 1997 [Sweden], Gotceitas et al. 1997 [Newfoundland]). Selection for complex environments is most likely density-dependent. In years of high settlement abundance, Grant and Brown (1998b) found more cod in non-eelgrass sites than previous years. Laurel et al (2004) found that young cod would aggregate over sand when eelgrass habitat was limiting. Therefore, the availability of refugia is more valuable in years of higher age-0 densities.

Not only is predator efficiency significantly reduced in complex habitats (Glass 1971, Mattila 1992, Lindholm et al. 1999), but survival rates of post-settled cod increase with rugosity (Tupper and Boutilier 1995b). Predator success is reduced in vegetation compared to less complex and barren areas most likely because of visual constraints imposed upon predators. This supports the fact that vegetation density is more important for reducing predation than length of vegetation (Lindholm et al. 1999). In complex areas such as cobble and rocky reefs, predator maneuverability is also limited compared to non-complex, uniform bottoms. Young fish tend to hide, but not feed, in these refuges (Helfman 1986), which have lower growth rates (Werner and Gilliam 1984, Lima and Dill 1990). Tupper and Boutilier (1995b) do, however provide evidence that young cod have the highest growth rates in eelgrass compared to sand, cobble and reef habitats. These fish exhibit apparent trade-offs between the prey-rich areas of slightly less structural complexity (i.e. eelgrass), which result in faster growth, and the refugia provided by more structurally complex habitats (i.e. reefs), which provided a greater chance of survival.

Post-settled cod are likely using complex habitats for cover from predators, such as cottids (Tupper and Boutilier 1995b) and gadids (Lindholm et al. 1999), including larger conspecifics (Bogstad et al. 1994, Grant and Brown 1998b, Linehan et al. 2001). In the lab, post-settled age-0 cod distribute themselves randomly, or show preference for sandy substrates over coarse substrates (Gotceitas and Brown 1993). This is expected since maneuverability and vision are reduced by additional complexity. When an actively foraging predator is introduced, age-0 cod associate with cobble or vegetative cover instead of sand or gravel (Gotceitas and Brown 1993, Gotceitas et al. 1995, Gotceitas et al. 1997) and are capable of distinguishing between foraging and non-foraging predators (Gotceitas et al. 1995, Gotceitas et al. 1997). In the field, predation is lowest and survival is greatest in cobble and rocky reefs, which are more complex than other natural substratum (Tupper and Boutilier 1995b). Linehan et al. (2001) demonstrated lower predation rates on age-0 cod prey in eelgrass than in non-eelgrass sites. Because post-settled cod prefer barren habitats over structural complexity unless they are threatened, it is reasonable to presume that they are not using complex habitats solely for prey acquisition.

Post-settled cod also exhibit behaviors associated with diel cycles. Diurnally, post-settled cod actively school and forage (Olsen and Soldal 1989, Grant and Brown 1998a) at times of the day when abundance of potential predators is low (Pihl 1982, Methven and Bajdik 1994, Grant and Brown 1998). Schooling facilitates detection of patchy food and also reduces the need for vigilance (Pitcher 1986). At night, post-settled cod cease feeding almost completely and disperse and hide (Grant and Brown 1998a, b) as conspecific predators move shoreward (Clark and Green 1989, Keats 1990, Pihl 1982). Some seek bottom habitats (Grant and Brown 1998a) or complex habitats (Grant and Brown 1998b). Grant and Brown (1998a) noted that fish migrating to the bottom might still feed, but predominantly on benthic prey. Predator avoidance behaviors like these provide benefits for foraging as well as minimization of predation risk. By reducing predation risk, fish can spend less time on vigilance and more time foraging.

2.5.2 Offshore Populations

Habitat selection is a primary subject in literature on the behavior of inshore individuals, but in the offshore, habitat is not as diverse. Frequently, rock and cobble are the only types of shelter available, because vegetation is predominantly absent due to lack of light availability. As in the nearshore, there is a considerable degree of spatial overlap between post-settled cod and their potential predators. Because these young fish are opportunistic feeders (at sizes <100mm), Lough et al. (1989) speculate that their absence from all other habitats besides pebble-gravel is a sign of predator avoidance. Cobble and pebble substrates may be preferred or survival may be greater in these habitats, because these habitats meld with their mottled coloration better than sand (Lough et al. 1989). The vertical relief offered by pebble and cobble also serves as refugia for fish in an otherwise exposed habitat. Inhabiting these untrawlable areas may also result in distorted abundance estimates (Gregory and Anderson 1997), and, in turn, the misinterpretation of behaviors.

In offshore waters, newly settled fish undergo limited nocturnal vertical migration up in the water column ~ 3-6 m from the bottom (Bottcher et al. 1998). This coincides with feeding on euphausids, in a zone where fish could drift passively in the bottom current at Georges Bank (Lough et al. 1989). At this stage, body coloration closely matches the substrate. Therefore, individuals are safer during the day when predators are most active. At night, conspecific predators are either inactive or not a threat (Linehan et al. 2001), making upward migration by juveniles less risky than during the day.

2.6 Conclusions

Despite the obvious importance of food and hydrography to the distribution of early juvenile stages of cod, the role that predators play cannot be ignored. Lima and Dill (1989) state it best; "...being killed greatly decreases future fitness". In the literature, there is evidence that food may not be limiting for young juvenile cod at various locations in space and time and at various life stages. In these instances, the distribution of young cod likely reflects the distribution of their predators.

The literature on anti-predatory behaviors demonstrated by inshore populations of post-settled cod has a strong emphasis on their use of structurally complex habitats. In particular, there has been considerable research conducted on the use of eelgrass habitats both in the lab as well as in the wild. Their affinity for these habitats has been demonstrated over many spatial scales and in many geographic locations.

Previously, less attention has been allotted to the relationship between predation potential and eelgrass patch structure at fine spatial scales. Recent research in landscape ecology emphasizes the relationship between habitat configuration and population-level dynamics. That is, the spatial layout of preferential habitats may be equally as important to the recruitment of young fish into the spawning stock as the quantity of habitat available. Prior to this thesis, the degree to which the geometry of eelgrass patches within these eelgrass sites influence survival remained untested.

Chapter Three - Habitat configuration affects predation risk: A study of newly recruited cod in eelgrass

3.1 Abstract

Post-settled age-0 Atlantic cod (*Gadus morhua*) seek refuge from predation in structurally complex eelgrass habitat in shallow, coastal nurseries. Lab experiments have demonstrated that predation risk on young fish is reduced in habitats of greater structural complexity compared to less complex or barren environs. To determine if predation risk is linked to the areal extent of coverage, I tested the hypothesis that predation risk of age-0 cod would decrease with increasing eelgrass patch size. During September and October 1999 and 2000, relative predation in tethered age-0 cod was quantified in eelgrass patches (1-80 m^2) at three sites in northeastern Newfoundland, Canada. Based on evidence of edge effects in terrestrial landscapes, I also tested the hypothesis that predation in eelgrass patches was elevated at the edge. I examined predation at 0, 5, and 10 m distances perpendicular to an 18 m long boundary between mud and eelgrass habitats at two sites in four biweekly sample periods in 2000. For all studies combined, 1,767 tether sets were made. Logistic regression analyses of odds ratios against patch-size show that intermediate-sized patches have the greatest percent loss at sites with overall moderate predation rates. This demonstrates that risk of predation decreases with area in patches larger than ~ 25-35 m^2. I also determined that predators respond to an edge effect within 10 m of eelgrass patch edges. I suggest that risk of predation decreases in patches > 25-35 m^2, because the prey, tethered in the centre of the patch, maintain a sufficient distance from the dangerous edge.

3.2 Introduction

Landscapes are comprised of mosaics of habitat patches, defined as contiguous, homogeneous structure at the finest available spatial scale (Nikora et al. 1999) with an ecologically meaningful edge that separates the patch from surrounding habitats (Fagan et al. 1999). Habitat patches are diverse in make-up and spatial scale. Species abundance, mortality or diversity may be closely linked to the amount of preferred habitat available and is often dependent upon faunal species or life stage, nature of the habitat, spatio-temporal scale of assessment (Eggleston et al. 1998) or local predator guild (Tewksbury et al. 1998). Furthermore, research stemming from anthropogenic fragmentation of terrestrial habitats demonstrates that the spatial layout of habitat patches may be more influential over population dynamics than the total amount of available habitat. Understanding predator response to fine-scale, aquatic habitat configuration could lead to indirect assessments of predator-related mortality in the recruitment of young fish. That is, predation could be estimated by assessments of landscape patterning – a parameter much more precisely quantified than natural predation.

Differential behavioral responses may also occur in particular areas within patches or microhabitats. For example, unique species interactions may occur at the edge region of two habitats of different structural complexities (Donovan et al. 1997). Edges function as a microhabitat between a less structurally complex area, which allows for greater vision and mobility necessary for prey searching, and a habitat of greater structural complexity, serving as refuge from predation. Young fish may seek edge zones so that they are in close proximity to cover while foraging. As a consequence of high prey fish (i.e. small fish) densities, edge zones may exhibit elevated risk, and they may also act as a 'line of travel' for predators in pursuit (see review in Andren 1995). The degree to which an edge effect penetrates the adjacent habitats is affected by species life history (e.g. extent of mobility, generalist/specialist, etc.), spatio-temporal aspects, and nature of the habitat involved. A correlation between edge effects and predation would allow us to identify landscape patterns that may exhibit higher risk of predation.

In their first vulnerable years, juvenile marine fish, including post-settled age-0 Atlantic cod, may inhabit structurally complex environments in shallow, nursery areas. In coastal habitats of the Northwest Atlantic, post-settled age-0 Atlantic cod are more abundant in complex areas (Tupper and Boutilier 1995b), particularly in eelgrass habitats (Gotceitas et al. 1997, Grant and Brown 1998b), which have been shown to reduce predator efficiency in the lab (Gotceitas et al. 1997). Young cod are able to assess the degree of predation risk between active and inactive predators (Gotceitas et al. 1995) and to select habitats that minimize predation risk (Keats et al. 1987, Lough et al. 1989, Gotceitas and Brown 1993, Fraser et al. 1996, Borg et al. 1997, Gotceitas et al. 1997, Gregory and Anderson 1997, Linehan et al. 2001). Predator-avoidance is critical due to the distribution overlap of these cod with predators such as older (1-3 year old) gadids, including conspecifics (Bogstad et al. 1994, Salvanes et al. 1994, Grant and Brown 1998a, Linehan et al. 2001), as well as cunners (Linehan et al. 2001), and sculpin (Tupper and Boutilier 1995b, Linehan et al. 2001). Despite higher predator densities in eelgrass (R.S. Gregory, unpublished data, 2000), predation risk on age-0 cod is lower in eelgrass than in less complex or barren habitats (Gotceitas et al. 1997, Linehan et al. 2001). Therefore, a loss or drastic change in such habitats could reduce the survival of young fish.

The purpose of my research was to examine the relationship between the predation risk of newly settled cod and the spatial configuration of individual eelgrass patches. I conducted two experiments regarding predation risk of post-settled age-0 cod within eelgrass habitats:

1) a patch-size experiment, in which I examined relative predation in eelgrass patches varying in size from 1 to 80 m^2, and

2) an edge effects experiment, in which I measured predation at 0, 5 and 10 m distances from the edge of an eelgrass meadow.

Based on evidence that eelgrass reduces predation risk, I tested the hypothesis that increasing the amount of refuge (i.e. increasing patch size) reduces risk of predation. To determine if predation varied by microhabitats within patches, I also tested for the presence of an edge effect by examining predation at the vertical, mud-eelgrass edge relative to predation in the surrounding, barren habitats. I anticipated that risk would be greatest at the edge and would decrease with increasing distance from the edge in the eelgrass direction. I expected that risk would be elevated in the mud locations. Predation risk was quantified using a tethering technique, which allows predation to be quantified on a relative scale (Heck and Thoman 1981, Wilson et al. 1987, Wilson et al. 1990).

3.3 Methods

3.3.1 Study Area

Newman Sound is a fjord in the southwestern waters of Bonavista Bay, Newfoundland, Canada (48 35'N, 53 55'W). Newman Sound (41 km by 1.5-3.0 km) is comprised of inner and outer portions, separated by a sill (18 m deep) approximately 7 km from the head of the fjord. The maximum depth of the inner sound is 55 m, whereas the outer sound reaches depths up to 300 m towards the open ocean. Newman Sound has a maximum tidal amplitude of approximately 1.5 m. In shallow areas within the sound (< 10 m deep), vegetation such as eelgrass (*Zostera marina*) provides vertical relief amongst the barren mud, sand and gravel substrates. Eelgrass is a subtidal flowering plant, which has an average blade length of approximately 0.75 m in Newman Sound (M.O, unpublished data, 2000). Eelgrass grows at varying densities as a mosaic of patches or as extensive meadows. As with most seagrasses, eelgrass beds fragment, contract and expand due to seasonal growth and die-off, storms (Preen et al. 1999), and anthropogenic impacts (Tveite 1984).

I chose five study sites within the study area. For the patch-size study, I identified three sites (P1, P2, and P3) with an abundance of eelgrass patches that were spatially distinct and varied in size (Figure 3.1). These sites were more than 4 km apart. For the edge effects study, I chose two sites (E1 and E2) (Figure 3.1) that had a distinct horizontal mud-eelgrass interface greater than 18 m in length, running perpendicular to shore (Figure 3.2). These edges were created as part of a concurrent eelgrass removal experiment, where divers had uprooted a 400 m^2 area of eelgrass, at 1.5-3 m deep, 10-60 m offshore, in the previous year.

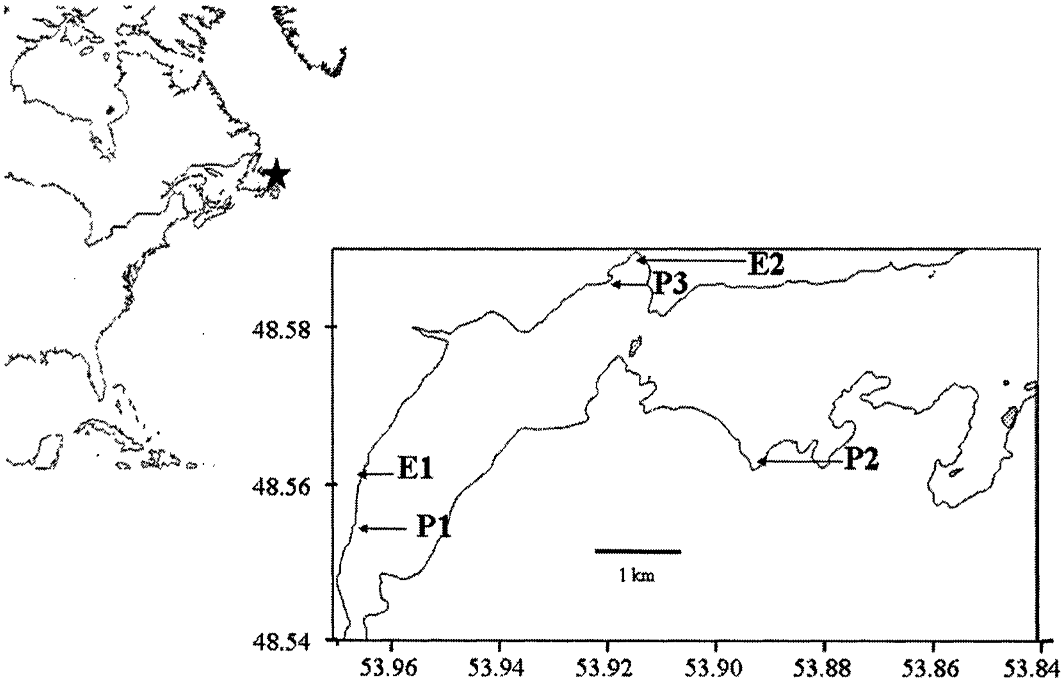

Figure 3.1. Study sites within Newman Sound, Terra Nova Park (inset; star on eastern seaboard map), Newfoundland, Canada. P1-P3 are patch-study sites. Edge effects study was conducted at E1 and E2. Scale of eastern seaboard map is 1:101,501,500.

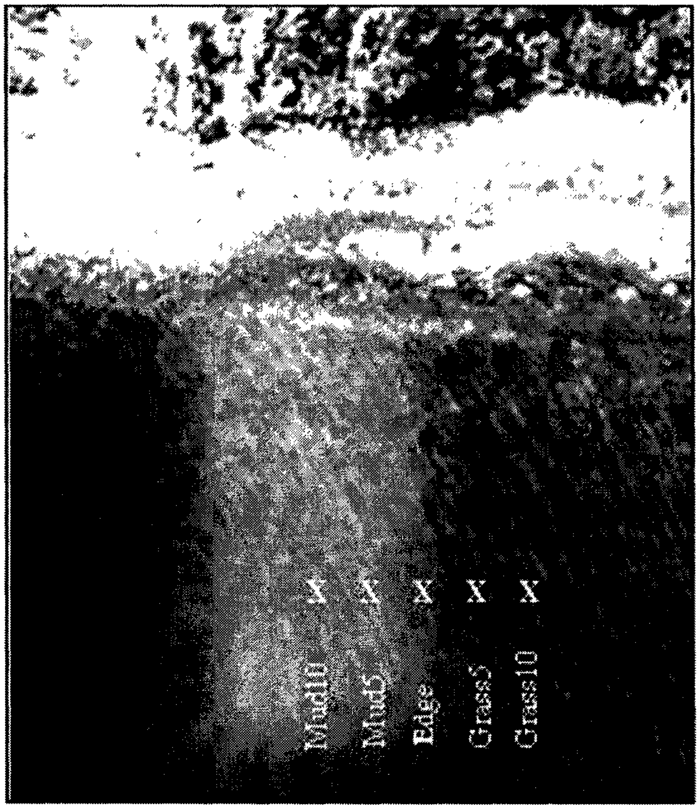

Figure 3.2. Edge sampling schematic. Relative predation risk was quantified using tethering. The edge effects study was conducted along a manipulated mud-eelgrass interface at two sites (aerial photograph of site E2 courtesy of R. Gregory). Tethering was done at 0 (Edge), 5, and 10 m increments in both the eelgrass (Grass) and Mud directions.

3.3.2 Tethering

Although tethering is a technique that has been used to study many species over the past twenty years, it has only recently been conducted using finfish (Curran and Able 1998, Danilowicz and Sale 1999, Linehan et al. 2001). The method consists of restraining or stabilizing a live prey item to measure predation risk in a localized area. Although not intended for the assessment of natural mortality associated with predation (Aronson and Heck Jr. 1995), tethering is a valuable method for examining the combined effects of predator abundance and motivation to feed (Post et al. 1998) and the encounter rate of predators and prey under different conditions or in different locations (Heck and Thoman 1981, Wilson et al. 1987, Wilson et al. 1990, Linehan et al. 2001).

In my experiments, I attached a live age-0 cod (45-105 mm standard length ((SL)) to a 0.5 m monofilament tether line (0.9 kg test) through the caudal peduncle with a #16 fly hook (~ 5 mm long) (Figure 3.3). The tether line was attached 0.25 m from the bottom of the placement line (11.4 kg test monofilament), which was anchored with a 0.9 kg lead weight and held vertical in the water column with a series of small floats. The top float acted as a site marker. This tether line allows the prey a 1.0 m diameter sphere of mobility and access to the substrate. A full description of the technique may be found in Linehan et al. (2001).

Each tether set was deployed with one prey fish for 15 minutes at the center of a patch in the patch-size study or at one of the five edge boundary locations in the edge study. Upon retrieval, I considered predation to have occurred (i.e. tether set was 'complete') if the tethered fish was missing ('fish gone' or 'hook gone'), or injured ('attack'), or if a predator was captured. Predators were identified to species, measured (± 0.5 cm SL) and released on site. A set was repeated or omitted if the prey was dead, but not attacked; because previous work showed that many predators did not attempt to forage on dead prey (Gregory and Levings 1998). Tether sets were also repeated or omitted if the line became tangled upon retrieval, which made it difficult to determine whether prey had either been attacked, eaten, or had simply been injured or freed during retrieval. Subsequently, I will refer to such sets that needed to be repeated or omitted as 'incomplete' tether sets.

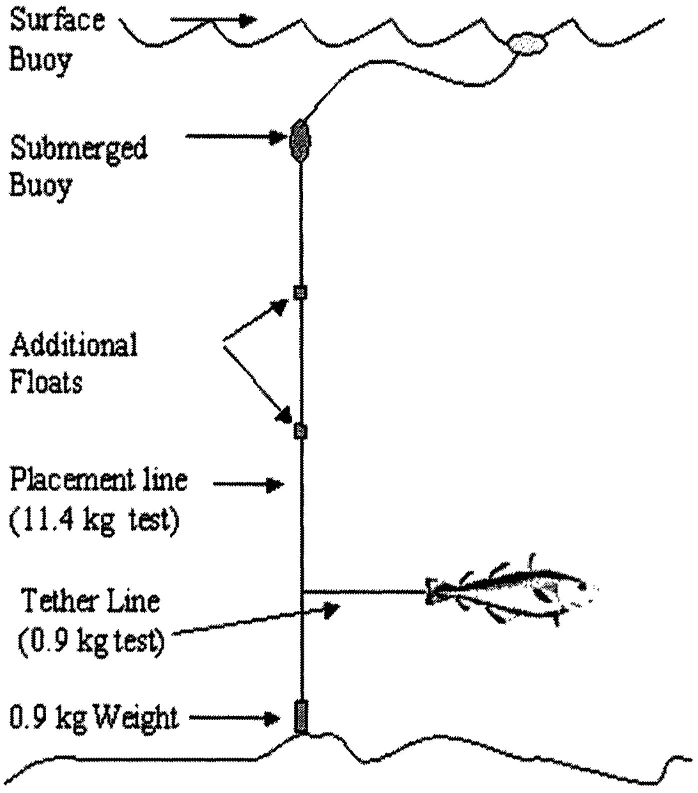

Figure 3.3. Schematic of a tether apparatus (~6.5 m from weight to submerged buoy) with age-0 cod prey (45-105 mm) attached to a 0.5 m tether line by a small hook through the caudal peduncle. Tether line is attached 0.25 m from the anchor.

Because predation of post-settled cod is known to be influenced by both light level and bottom depth (Linehan et al. 2001), tethering was conducted during daylight hours (900-1800) within a narrow depth range of approximately 1.5 m, corresponding to the maximum daily tidal range. Exact patch depth range depended upon the site: P1 (4.3-5.2 m), P2 (4.9-6.1 m), and P3 (5.2-7.3 m). In the edge experiment, tethering was conducted at depths of 2.0-2.5 m. I acquired prey from non-sampling sites within the sound using a seine. Prey fish were held in 20-liter holding tanks during tethering operations. Rock cod (*Gadus ogac*) were used in approximately 50% of all tether sets because they were equally abundant in seine collections and are difficult to distinguish behaviorally (Laurel et al. 2003) and visually (Methven and McGowan 1998) from Atlantic cod at this stage.

3.3.3 Patch-size experiment

Approximately five patches in each of three size classes, small (1-5 m^2), medium (6-10 m^2), and large (11-56 m^2) were marked in each of the three coves (P1-P3) for a total of 40 patches in 1999. Patch size refers to the areal extent of a patch, which was visually estimated during SCUBA surveys. Divers took visual estimates of the area of each patch to the nearest 1 m^2. Twenty-six additional patches were marked in one cove in 2000. I chose patches absent of large barren areas or boulders, separated from the nearest patch by more than 2 m, and that were within the designated depth range per site. Patch markers consisted of two small floats, tied to 6-7 m polypropylene rope, anchored with a construction brick. I secured one float at the high tide mark and one at the low tide mark, thereby keeping the line taut and allowing at least one marker to be visible from the surface throughout the day. To prevent entanglement with tether lines, I offset the markers two meters in a designated northerly or southerly direction from the approximate center of the patch.

I tethered each patch 10 times during each of 3 sample periods September 28-October 28, 1999, for a total of 1200 sets (10 repetitions x 3 sample periods x 11-15 patches per location x 3 locations). In 1999, sample periods were divided as follows: late September (September 28-30), mid-October (October 13-25), and late October (October 26-28). Patches ranged from 1-56 m^2. The study was repeated at P3 in the following year: mid-October (October 6-25, 2000). In 2000, I sampled 26 patches in a single cove and a broader patch size-range (1-80 m^2). A total of 208 tethers (8 replications x 26 patches) were attempted in 2000. Overall, a total of 1277 tether sets were completed. This total does not include sets that were considered 'incomplete' (e.g. prey fish was dead upon retrieval).

3.3.4 Edge effects experiment

At E1 and E2 (Figure 3.2), tether lines were set at the "Edge", and at 5 m intervals from the Edge in both directions (i.e., into the mud and the eelgrass areas). Locations are referred to as Grass10 (10 m from Edge), Grass5 (5 m from Edge), Edge, Mud5 (5 m from Edge), and Mud10 (10 m from Edge) (Figure 3.2). I tethered each location ~12 times during four biweekly intervals (periods 1-4) between August 24 and October 5, 2000. A total of 490 tether sets were completed (12 repetitions x 2 sites x 5 locations x 4 sample periods + 10 tethers that were inadvertently conducted in addition to 480 that were planned). Because the patch study occurred in deeper water, the sets were more likely to tangle. Therefore, a greater percentage of tether sets were completed in the edge effects study than the patch study.

3.3.5 Data Analyses

I analyzed relative risk of predation using the Odds Ratio (OR), defined as

$$OR = (p_I / (q_I) / (p_0/q_0) \qquad 3.1$$

such that p_I is the proportion of tether sets where predation was observed divided by q_I, which is the proportion of sets without predation. $p_0$and q_0 are proportions of sets with predation for the reference class (i.e. the smallest patch in the patch-size study or Grass10 in the edge effects study).

In the patch size experiment, I quantified the change in risk relative to patch area (A), sample period (P), and site (S). The model was:

$$\text{Ln } OR = \beta_o + \beta_S{*}S + \beta_P{*}P + \beta_A{*}A + \beta_{A*S}{*}A{*}S + \beta_{A*P}{*}A{*}P \qquad 3.2$$

for 3 sites, during 3 periods, in areas from 1-80 m^2. Logistic regression was used for these analyses because of the binomial distribution of the data (i.e. predation event or no predation event). Each parameter β quantified the change in risk due to the factor or the factor interaction. For example, $e^{(\beta_A{*}A)}$ (or $\beta_A{*}A$ for the logistic regression) was the change in relative risk (OR), multiplied by the change in area. For this analysis, the reference odds were those for the smallest patch size.

Change in risk relative to patch depth (De) was quantified according to the model:

$$\text{Ln OR} = \beta_o + \beta_{De}{*}De. \tag{3.3}$$

For the edge experiment, the model for change in risk relative to location (L) (i.e. Grass10, Grass5, Edge, Mud5, and Mud10), sample period and site was:

$$\text{Ln OR} = \beta_o + \beta_S{*}S + \beta_P{*}P + \beta_L{*}L + \beta_{L*S}{*}L{*}S + \beta_{L*P}{*}L{*}P \tag{3.4}$$

at 2 sites, during 4 periods, at 5 locations. I also quantified the change in risk relative to distance (DI) from the edge according to the model:

$$\text{Ln OR} = \beta_o + \beta D_I{*}D_I, \tag{3.5}$$

where Distance was 0, 5, or 10 m from the edge and did not include substrate.

For both experiments, parameter estimates were determined by using a binomial error structure (log link; proc GENMOD) in SAS (Release 8.0). I examined changes in Chi-square values to determine the significance of the additional variables. Bootstrap estimates (Manly 1991) were used to establish 95% confidence intervals. All means are reported with standard deviations.

3.4 Results

3.4.1 Patch experiment

Predation was observed in 45% of all tether sets (N=1277) in the patch size experiment. Predators were captured in 28% (N=159) of predation events. Of predators captured, rock cod were most abundant (51%), followed by sculpin (25%), cunners (15%), and Atlantic cod (9%). The mean predator SL was 22.0 ± 6.3 cm (range 11.0-50.0 cm).

In 1999, predation at each site varied greatly between sample periods and increased with time at P2 and P3 (Table 3.1). The greatest numbers of predation events (65 - 80%) were recorded at P3, while predation at P1 remained consistently low (5%, 11%). I found predation at P2 (33%, 58%) to be marginally lower than at P3. There was a significant interaction effect of site and period on predation risk ($\chi^2 = 7.95$, $p = 0.0188$, df = 2, N = 1127 sets). Therefore, I could not pool patch-size predation data among sites and periods. I separated the data by site and period prior to further analysis. My revised model was:

$$\text{Ln OR} = \beta o + \beta A * A \qquad 3.6$$

for each period at each site. During mid-October in 1999, I found predation risk significantly increased with patch area at P2 ($\chi^2 = 8.9743$, $p = 0.0027$, df = 1, N = 137 sets) and at P3 ($\chi^2 = 6.4268$, $p = 0.0112$, df = 1, N = 124 sets) (Figure 3.4 (d, e)). Predation risk increased with patch area at P1 (throughout October) (Figure 3.4 (c, f)), and in late October at P3 (Figure 3.4 (g)), but the increase was not statistically significant. No trend was apparent at P1 and P2 in late September (Figure 3.4 (a, b)).

Table 3.1 Percent loss of age-0 cod to predators during the patch-size study in natural eelgrass patches 1-80 m^2 (N=1277). Predation levels were quantified using tethering, which assesses relative predation risk and not natural predation rates. Statistical conclusions apply to OR. *Denotes sampling during 2000, whereas all other sampling was conducted in 1999.

Site	**Sample Period**	**Percent Loss**
P1	Late September	5
	Mid-October	11
	Late October	5
P2	Late September	33
	Mid-October	58
P3	Mid-October*	65
	Mid-October	68
	Late October	80

In 2000 (Figure 3.4 (h)), patches as large as 80 m^2 were examined. High variability in patches less than approximately 25 m^2 was apparent when predation risk (OR) was regressed against patch area. In patches greater than 25 m^2, risk decreased with patch area. Intermediate-sized patches were the riskiest. This relationship was best described as a parabolic function of patch area:

$$\text{Ln OR} = 0.3022 + 0.0572\ (A) + -0.0009\ (A^2) \qquad 3.7.$$

(A^2, p = 0.0039; A, p = 0.0170).

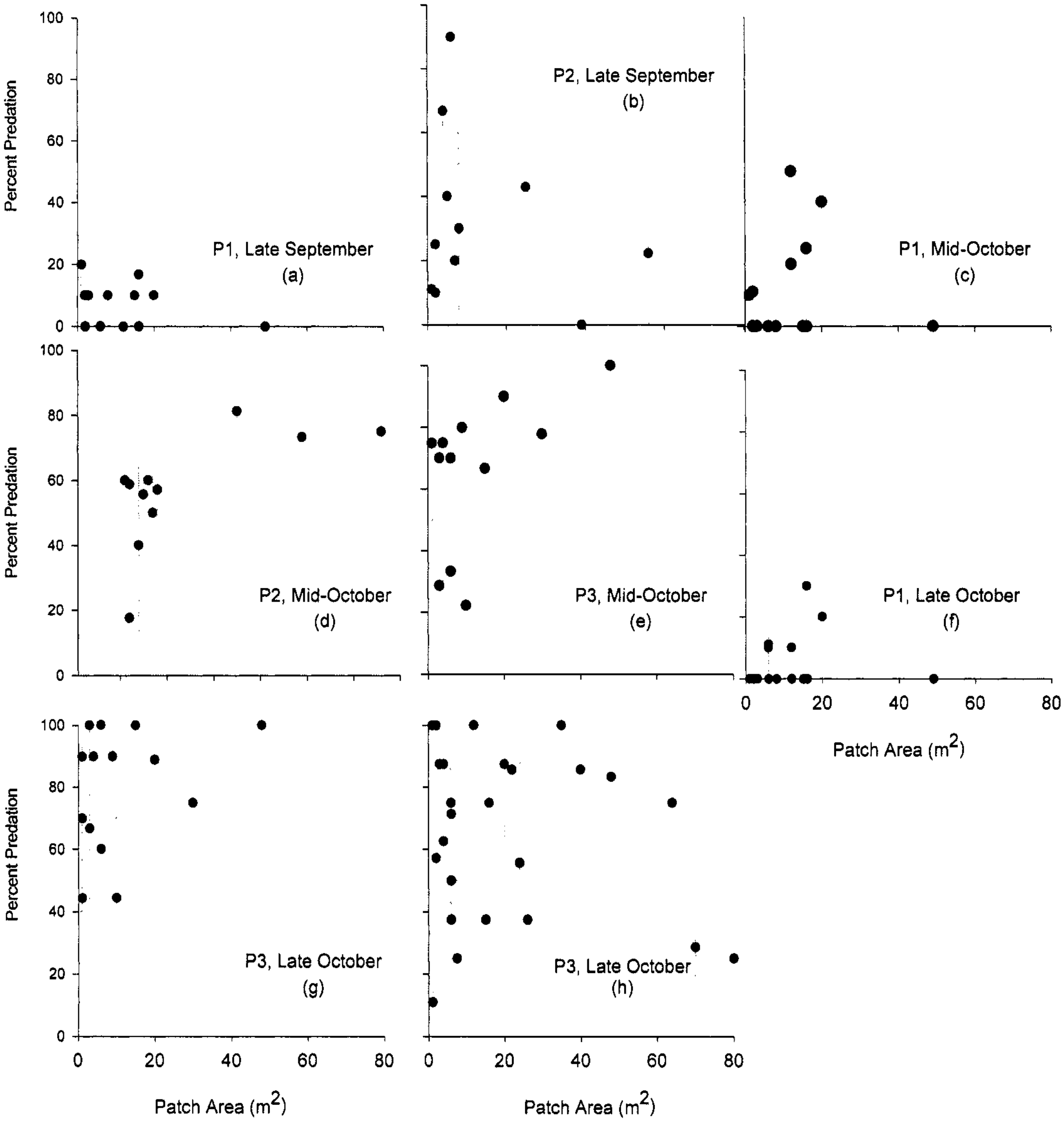

Figure 3.4. Percent loss of tethered fish at sites P1-P3 in September 1999 (a, b), mid-October 1999 (c-e), late October 1999 (f, g) and late October 2000 (h). Each point represents ~7-10 tether sets. Ninety-five percent confidence intervals are based on bootstrap estimates.

To ensure that risk was independent of depth, I examined the effect of adding patch depth to the model. The site by depth interaction term was not significant ($\chi^2 = 2.09$, $p = 0.3520$, df = 2, N = 960 sets) for the two sites (P1 and P3) examined. Data from P2 were excluded from this analysis, since depth of individual patches was not recorded. Site P2 had a narrow depth range (4.9-6.1 m) that fell within the extent of depths at P3 (5.2-7.3 m); therefore, I assume that depth did not influence predation risk at P2.

3.4.2 Edge effects experiment

In the edge effects experiment, I observed predation in 39% of tether sets (N=490) and captured predators in 34% (N=64) of predation events. Of these sets, rock cod were caught most often (47%), followed by cunners (31%), sculpin (19%) and Atlantic cod or hake (2%). The mean predator standard length was 16.4 ± 2.8 cm (range 11.5-23.0 cm). Smaller predator sizes in this experiment compared to those in the patch-size experiment are attributed to the shallower depth at which this experiment was conducted, consistent with Heinke's Law (i.e. small fish are found in shallow water – Cushing, 1975).

Predation events varied from 7-100% at each site-period (Table 2.2) and were higher on average at E2 (57%) than at E1 (23%). Percent loss decreased consistently at each site over time at relatively similar rates ($\chi^2 = 0.16$, $p = 0.6903$, df = 1).). Risk was significantly lower in Mud than in Grass overall ($\chi^2 = 6.84$, $p = 0.0089$, df = 1) and depended on distance from the edge ($\chi^2 = 17.35$, $p = 0.0002$, df = 2). Among sample periods and sites, predation in the edge habitat was consistently higher than points 5 and

10 m away. This result was independent of site ($\chi^2 = 4.08$, $p = 0.1299$, df = 2) and period ($\chi^2 = 5.29$, $p = 0.507$, df = 6).

Table 3.2 Percent loss of age-0 cod to predators along a vertical mud-eelgrass edge during the edge effects study from August 24 - October 5, 2000. (N=490). Predation levels were quantified using tethering, which assesses relative predation risk and not natural predation rates

Site	Sample Period	Percent Loss
E1	1	29
	2	25
	3	28
	4	7
E2	1	100
	2	63
	3	31
	4	35

Data were divided by site but sample periods were grouped. This is because OR was significantly different by location within a site ($\chi^2 = 17.91$, $p = 0.0013$, df = 4), but not between sample period and location ($\chi^2 = 9.77$, $p = 0.6360$, df = 12). The revised model at both sites was:

$$\text{Ln OR} = \beta_o + \beta_P{*}P + \beta_L{*}L + \beta_{P*L}{*}P{*}L. \qquad 3.8$$

According to this model, relative risk at the edge was greater than all other locations at both sites, except for Grass5 at E2 (Figure 3.5), but the differences were not significant. See Appendix A for a comprehensive list of p-values.

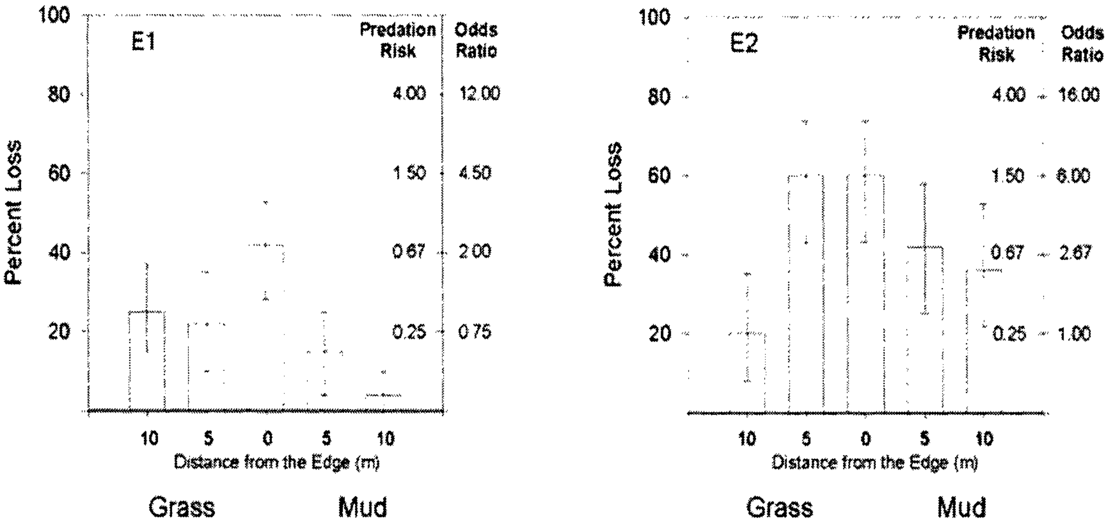

Figure 3.5 Percent loss of tethered fish at the edge treatments at each of the two sample sites (E1, E2) in the edge effects study (N=490). Edge is represented by distance of '0'. Each bar represents 35-56 tether sets. Ninety-five percent confidence intervals are based on bootstrap estimates. Odds Ratio is the Predation Risk relative to odds of risk at Grass10 (where OR=1) at each site.

3.5 Discussion

3.5.1 Predation and structural complexity

Structural complexity has repeatedly been linked to reduced predator efficiency (see review in Nelson and Bonsdorff 1990). The results of small-scale laboratory experimentation have suggested greater overall structural complexity of habitat would be beneficial for survival in such places as inshore nurseries, where young fish seek refuge from predation. In the patch-size study, I tested the hypothesis that larger patches of natural eelgrass would have lower risk of predation than smaller patches.

In mid-October at sites P2 and P3, I found the opposite to be true – predation increased significantly with patch size (up to 56 m^2) (Figure 3.4 (d, e)). It is likely that this relationship was not significant at site P1 because of the low overall occurrence of predation (7%) at this location during this study. This means that predation was so low that no patches were undergoing high levels (>50%) of predation. Although, of the patches that did undergo predation events at this site, predation did increase with patch size in mid- and late October (Figure 3.4 (c, f)) except at the largest patch (49m^2). Of the tethers set at this large patch throughout the study (N = 28), not a single predation event occurred. Other fine-scale physical (e.g. neighborhood effects, temperature or salinity anomalies, etc.) or biological (e.g. increased prey abundance, etc.) variables may explain the lack of predation at this patch, although this is only speculation due to the lack of such data in this study. Of the two remaining samplings in 1999, no trend was apparent at P2 in late September, which may also be a result of relatively low predation (33%) at this site during this sample period. Conversely, the high occurrence of predation (80%) at P3 in late October may result in the lack of relationship between patch size and predation. That is, predation events were occurring at such high rates during this sampling that it is not possible to differentiate between variables and all patches had high rates of predation. For this reason, further results will be discussed with respect to overall predation by site by sample period that was occurring at intermediate levels unless otherwise stated.

The results from the samplings in 1999 indicate that, at intermediate levels of predation (58 - 68%), it is possible to detect a relationship between patch area and risk of predation and that this correlation is positive. These initial results appear contrary to the original hypothesis that an increase in structure should reduce predation risk. The complicating factor is that young fish are attracted to complex areas and so, in turn, are their predators. Therefore, depending on the ratio of predators to prey, highly complex habitats may serve as areas of greater overall predator activity. This is supported by work conducted by Laurel et al. (2003b) in which predator densities were at least twice as high in large patches (22 m^2) compared to small patches (< 11 m^2). It is unlikely that increasing patch structure would actually improve predator efficiency (e.g. by increasing visibility or maneuverability) based on behaviors demonstrated by predators in laboratory tests (Glass 1971, Cooper and Crowder 1979) but, larger patches may have higher abundances of predators, resulting in greater risk of predation per tethered individual.

The data from sampling at P3 in late October in 2000 result in a statistically significant correlation between predation and patch size, although the relationship for this data, which includes larger patches (up to 80 m^2) than the 1999 datasets (up to 56 m^2), is parabolic (Figure 3.4 (h)). This means that there is increasing predation with patch area in patches up to ~35 m^2 in area, which is consistent with the 1999 data. However, in patches larger than ~35 m^2, predation decreases with patch size as I had originally hypothesized. Although there is a considerable amount of variability in predation in the smaller patches in the 2000 dataset (Figure 3.4 (h)), the decrease in predation in patch sizes >35 m^2 is distinct. The overall predation rate for this sampling (65%) can also be classified as undergoing intermediate predation (58 - 68%) as did the two aforementioned statistically significant samplings in 1999. While the 1999 data support that larger patches have increased predation risk, the results from the edge effects study further the explanation of what is occurring in patches >35 m^2 in the 2000 data.

3.5.2 Predators respond to edge effects

In the edge study, I expected risk to be higher at the less structurally complex Mud locations than at the edge, since structure reduces predator efficiency. The center of the patch (i.e. Grass10, the core area with the most surrounding cover) was expected to provide the best protection. In this study, I found the edge to be more dangerous than the surrounding mud and interior eelgrass habitats and that risk decreased with distance from the edge. One explanation for this is that the 'predators' in these experiments are actually 'prey' themselves. Even though the Mud environs may be theoretically easier to hunt and attack prey than the eelgrass, these 'predators' may also need to seek the shelter of eelgrass patches to avoid being preyed upon themselves. Therefore, these predators may be searching eelgrass edges because edge habitats provide both the safety of cover and the ease of hunting associated with less structurally complex habitats.

This result is supported by research demonstrating higher predation at habitat edges, primarily regarding avian nest predation (Andren and Angelstam 1988, Donovan et al. 1997). There is also evidence that predators search the top edge of eelgrass patches for cod prey and that prey also hover over these edges (R. S. Gregory, unpublished data, 1999, Laurel 2003a). Gregory examined predation within the patch (0.25 m from the bottom), on the top edge of the grass (0.75 m from the bottom) and well above the grass (1.5 m from the bottom) and found that the highest predation rates occurred at the top edge of the eelgrass. Of young cod (i.e. prey) caught at 'non-eelgrass sites' that bordered eelgrass areas, Laurel et al. (2003a) conducted snorkel surveys and found that these fish actually inhabit the edge zone at the eelgrass boundary of the 'non-eelgrass' location. Elevated predation risk per tethered individual at these eelgrass edges is most likely a result of increased predator and prey activity.

In this edge effects study, I also found slightly higher predation in Grass (38%) than in Mud (32%). Again, this was contradictory to my original hypothesis that structure would reduce predation. At first glance, this result further supports the data from the patch-size study that increasing the amount structure (or patch size) results in greater predation, which I attribute to predators being drawn to refuge by prey in addition to predators seeking areas of refuge themselves. However, the edge effects data at 10 m from the edge would correspond to a patch size well-beyond the largest patch sampled (10 m radius; $A = \pi r^2 = 314\ m^2$), which should have extremely low predation if the model from the 2000 data was applied to data from distances 10 m from the edge. This discrepancy may a result of slightly different behavioral dynamics of predators because the study area in the edge effects study more closely resembles an extensive meadow of eelgrass than a large, natural patch due to its rectangular and distinct configuration (Figure 3.2). Furthermore, the Mud area surrounding this meadow is considerably more expansive than natural barren areas near patches in the patch-size study. The result may be that the barren areas may be more devoid of prey than in normally configured barren areas between patches, because of the lack of nearby refuge. Predator and prey densities may be elevated in the nearby Grass areas for the same reason. Therefore, the quantitative models from the patch-size experiment may not apply directly to the edge effects data. This notion is further described in the following section.

3.5.3 Integrating the results

Under intermediate levels of predation, patches of 35 m^2 underwent some of the highest levels of predation; however the expected decrease in predation risk did occur in patches greater than 35 m^2. In patches greater than this size, the prey, centered in the patch, can find safe haven from predators that are roaming the dangerous edge. Predation risk decreases with increasing patch area beyond this size, perhaps because the tethered prey reach a safe distance from the dangerous edge. Predators of age-0 cod are attracted to larger patches of eelgrass, which most likely have greater prey abundances, but they also appear to be negatively affected by patch size beyond a threshold. Beyond a threshold patch size, it may be more efficient for predators to search the edges for prey than to traverse the patch core, which would limit sight and mobility. In the edge study, the edge effect was diminished at some locations 5 m from the edge. Consequently, the edge effect should decrease before patches approach ~ 78.5 m^2 (Area = πr^2; r = 5 m, for Euclidean shapes), which roughly corresponds to our largest patch size of 80 m^2. Therefore, the centers of the largest patches are the safest areas for young cod to inhabit. However, total area of natural seagrass patches with 5 m radius would probably be smaller, because they have interior corridors and more convoluted perimeters. Also, in Euclidean-shaped objects, perimeter to area ratio decreases with increasing area. That is, the amount of edge per unit of area decreases as size of Euclidean-shaped patches increases. Because risk increases at edges, I could expect predation to decrease with patch area (less edge per unit area). Eelgrass patches are not Euclidean and hence it would be interesting to examine the relationship between predation risk on 0-group cod and perimeter to area ratio of eelgrass patches. Based on my results, I expect patches with more edge (perimeter) and intermediate size (area) to be the most dangerous.

A negative correlation between predation and patch-size is consistent with work done by Irlandi (1997) on hard clam (*Mercenaria mercenaria*) survivorship in natural seagrass patches (~1-10 m diameter). Irlandi also found a positive, although insignificant, correlation between survival and shoot density and below-ground biomass. In a subsequent study, Irlandi used artificial seagrass to control for shoot density and below-ground biomass and found no difference in survival between patches of 2 m^2 and 16 m^2. Therefore, she attributed increased survival of hard clams in larger, natural seagrass patches to the difference in structural characteristics of seagrass patches - as opposed to areal extent. Gotceitas et al. (1997) showed that young cod use eelgrass independent of shoot density, although the latency period until capture increased with density. Based on my method of patch selection, shoot density can be eliminated as a confounding variable. I intentionally chose patches of visually similar densities, absent of large barren areas or boulders. One concern regarding shoot density could be that larger patches had some unvegetated corridors that could serve as pathways of predator travel. The edge effects results dismiss this issue, though, because corridor boundaries would act as edges, thus elevating predation in larger patches.

The edge effect may provide an explanation for the noticeable degree of variability in predation risk in the smaller patches at some locations. Because fish within a small patch were always close to the lateral edge, these patches would be most easily influenced by neighboring patches. For example, a small patch located near an intermediate-sized patch undergoing high predation may undergo higher predation than a small patch near another small, predator-free patch. Surrounding habitat types could also be more influential over risk in small patches. That is, a patch near a barren microhabitat may have very different risk than a patch of the same size near a rocky reef. This is supported by work conducted by Laurel et al. (2003b), where mud had greater predation rates than eelgrass, but the authors suggested that this was affected by the close proximity of the mud sampling locations to refuge. Overall, it may be beneficial to determine the minimum patch size whose predation rate would not be affected by its surroundings, and for patches smaller than this minimum, nearest neighbor or neighborhood analysis should be conducted.

Interesting comparisons can be made between these studies (i.e. patch-size and edge effects) and those conducted by Laurel et al. (2003b). In tethering conducted on artificial eelgrass patches during autumn 1999 and 2000 in Newman Sound, Newfoundland, Laurel et al. found that predator densities were similar in patches 0.32 – 11 m^2 and that predation risk decreased with patch size within patches of this size range. Over this range of patch sizes in my experiment, there was a considerable degree of variability in predation risk. The overall predation rates for the Laurel et al. experiments were considerably low (9% and 16%) and were closest to predation rates at my site P1 (5-11%) where no significant trends in predation and patch size were found throughout the season. Laurel et al. also found that predator densities were twice as high in the largest patches ($22m^2$) compared to the smaller patches and this corresponded with elevated predation. This is consistent with my assumption that predation risk was increasing in patches up to ~35 m^2 in my study locations because of increased predator densities. By eliminating the largest patches from their analysis and thus controlling for predator density, Laurel et al. were able to demonstrate that increasing patch size does reduce predator efficiency, which is consistent with the results that I demonstrated over the largest patch sizes at much higher levels of overall predation (58-68%).

Although many studies demonstrate that eelgrass may be preferred by young cod (e.g. Gotceitas et al. 1997, Laurel et al. 2003a, Laurel et al. 2004), this is a density-dependent relationship (Laurel et al. 2004). When eelgrass habitat is limiting, numerous studies have demonstrated that young cod use rocky reefs, boulders or macroalgae as means of protection. Laurel et al. (2004) have even shown that young cod will disperse into sand habitats and then form tight schools as a means of predator avoidance when optimal habitat is not available. The results of the patch-size and edge effects studies may be extrapolated to other structurally complex habitats. What the patch-size and edge effects studies demonstrate is that increasing the amount of refuge can actually increase predation risk in what were previously believed to be 'safe' areas and that the edges of refuges are likely to have elevated risk of predation. Perhaps more importantly, these studies show that these relationships may not scale-up linearly and that more complex dynamics may occur at each additional increase in spatial or temporal scale.

3.5.4 Temporal component

In the edge effects experiment, overall predation at each site generally decreased from late August through early October; although, there was a general increase in predation from late September to late October in the patch-size study. The ratio of predator to prey size may be one explanation for these predation trends. I compared the size of tethered prey to predator sizes taken from a concurrent seining study conducted at sites adjacent to P1, P2, P3, E1 and E2 for corresponding sampling dates in 1999. See Methven and Schneider (1998) for a full description of the beach seine methods. I considered 'predators' to be Atlantic cod, rock cod, hake, cunners or sculpin greater than 110 mm SL, corresponding with species and minimum length of predators caught on tether lines. I found that the overall predator to prey size ratio was lower (i.e. prey were closer in size to predators and presumably more difficult to eat) in the edge effects study (2.18) than in the patch-size study (2.30). When these ratios are broken down by sample period, there is a general decrease in the predator to prey size ratio in the edge effects study (2.18, 2.19, 2.16 and 2.13 for periods 1-4, respectively), corresponding with decreasing predation in this study, and increasing ratios in the patch-size study (1.78, 2.41, and 2.78 for periods 1-3 in 1999), which corresponds with increasing predation in this study. It is welldocumented that the smallest fish are not always at the greatest risk for a variety of reasons (Sogard 1997), and this includes the fact that small fish may be too large for their predator's gape and may be at greater risk late in the season as predator size increases at a faster rate than their prey sizes do – for some species.

Another possible explanation for these trends in predation is that as the predators grow they move from shallower waters (edge effects study) to deeper waters (patch-size study). This is supported by greater mean SL of predators caught in the patch-size study (22.0 cm) compared to the edge effects study (16.4 cm) and by the relationship between average patch depth and percent prey loss at P1-3 in the patch-size study, which is also consistent with the results of Linehan et al. (2001). Falling temperatures in shallower environments may also drive predators offshore. In addition, higher temperatures earlier in the season may result in decreased predation because summer temperatures may be at the upper end of the optimal temperature range preferred by these northern fish species. If the data are combined seasonally between the two studies, there are two peaks of high predation rates – one that occurs in late August and one that occurs in late October. This loosely corresponds to two pulses of age-0 cod settlement that occur each autumn at the study sites (Gregory et al. 2002), which would also support the evidence that predators may be attracted to areas of greater prey densities.

There was also a high degree of variability of predation rates within a given sample period. On a day-to-day basis, predation could vary from 100% to about 75% or less. On days where the first 2-3 sets on a series of 5 patches (i.e. 10 - 15 sets out of 100; 85-90% total predation at that site for that period) all underwent predation, sampling was discontinued and sets were not included in the total of completed sets. This was done because no difference could be detected between variables at these high rates of predation. That is, there would be no difference in predation risk between patches of different sizes or at different edge locations when the overall rate of predation was 100%. Therefore, the patterns of patch and edge use may only hold true for periods of intermediate (i.e. ~58-85%) predation.

3.5.5 Validation of the tethering technique

To examine the effects of attraction to tethering sites, I analyzed a portion of the dataset (10 patches) to determine if the last five sets at a given patch had different predation risk than the first five sets. I used data from P2 on October 25, 1999, since predation was intermediate and all patches were sampled ~10 times in one day. Results show that relative risk during the second five sets did not differ significantly from risk during the first five ($\chi^2 = 0.611$, $p = 0.4331$, df = 18, N = 98 sets). Therefore, I conclude that predation risk does not increase with each additional tether set (up to 10 sets).

I compared my data to data from the previously mentioned seining efforts to examine whether a representative community of predators captured the tethered prey. I used the previously described definition of 'predators' for these calculations. Using a contingency test,

$$G = 2\Sigma(f_o(\mathrm{Ln}(f_o/f_e))) \qquad 3.9,$$

where G was the goodness of fit, f_o and f_e were the observed and expected frequencies of predators, respectively. The proportion of predator species in the seine hauls was similar to those captured by tethering if hake were eliminated from the contingency test ($G = 4.2187$, $p = 0.238$, $df = 3$, $N = 4$ species). Hake were under-represented in tethering studies compared to seine studies, indicating that age-0 cod were not preferential prey items for young hake in Newman Sound in 1999 and 2000. Lastly, because predator species, size of predator, and the type of predation event (hook gone, fish gone, and attack) were independent of patch area and edge treatment, the results from both experiments were not driven by a single predator species or size at the spatio-temporal scales that I studied.

I also examined the effect that prey species and size had on the likelihood of undergoing a predation event. Rock cod were used as surrogates for Atlantic cod in approximately 50% of all tethers set. I found that rock cod were preferred by predators by a negligible 6% ($N = 1767$) over Atlantic cod, thus supporting the assumption that post-settled, age-0 rock cod were sufficient surrogates for Atlantic cod in predation studies in coastal Newfoundland. Although tethered prey ranged in size from 48-105 mm, 90% were 55 to 96 mm long. There was a bimodal distribution with modes at sizes of 66 and 93 mm. Using logistic regression analysis (Logit model), I found that there was no correlation between size of the tethered prey and the odds of a predation event ($\chi^2 = 0.92$, $p = 0.34$, df = 1106, $R^2 = 0.001$). This demonstrates that predators in this study were not selectively attacking tethered fish based on size.

3.6 Conclusion

In conclusion, predators of post-settled age-0 Atlantic cod appear to respond to the spatial distribution of eelgrass in coastal nurseries. Because predation increased with patch size, I speculate that predators are attracted to areas of greater prey. However, beyond a threshold size, predators are responding to an edge effect. That is, tethered fish, centered in large patches, are safe from edge-searching predators. These results provide insight into the behavioral responses of predators to local landscapes.

Chapter Four – Predation risk with respect to morphology of individual eelgrass patches

4.1 Abstract

The population dynamics of some species are linked to the spatial configuration of their preferred habitats. Results from the experiments in Chapter 3 demonstrated that predation risk of post-settled age-0 Atlantic cod depends on eelgrass patch size as well as distance from the edge of eelgrass patches. Knowing that patch area and patch edge are important to predation potential, it is likely that patch shape, or the amount of edge per area, would also be relevant factors to the predation risk of young fish. In this experiment, I used underwater videography to create images of 18 individual eelgrass patches at one cove in Newman Sound, Bonavista Bay, Newfoundland, Canada. I quantified the perimeter and area of each patch at 5 different resolutions using two variations of the box-counting method. Using this relationship across resolutions, I was then able to calculate a measure of the structural complexity – the fractal exponent – of individual eelgrass patches. I examined the relationship between patch perimeter, perimeter to area ratio and fractal exponent to predation risk of each patch. I found no correlation between these patch shape values and risk of predation. I believe this observation may be a result of the techniques that I used; further study is needed to reject the hypothesis that patch shape is an important factor in predation risk of age-0 cod.

4.2 Introduction

There is growing interest in the link between the population dynamics of a species and the spatial layout of preferred habitat. These relationships are being examined from broad (regional) to intermediate (landscape) to small (microhabitat) scales. Across scales, habitat is being quantified for comparison in a variety of ways; including examinations of structural complexity (see Beck 2000 for a review of techniques). Different calculations of fractal analyses, in particular, are used to quantify landforms in a variety of different ways including estimation of the relative 'edginess' of individual patches within a landscape (Kenkel and Walker 1996).

The results from the Patch-size and Edge Effect studies led me to believe that the shape of eelgrass habitats would affect predation rates. I measured the fractal dimension of individual eelgrass patches from the year 2000 dataset (Chapter 3, site P3) using underwater video combined with a box-counting technique. The fractal dimension gave me a quantification of perimeter to area ratio with respect to the resolution at which these quantities were measured. I used tethering to relate predation risk of age-0 Atlantic cod to the fractal dimension of eelgrass patches. I anticipated that more fractal, or convoluted, patches would have higher predation rates, based on the assumption that more perimeter (i.e. more edge) would be more dangerous.

4.3 Methods

4.3.1 Study Area

I selected eelgrass patches in Mistaken Cove (P3 from Chapter 3), where patches were abundant, distinct and varied in size. Patches ranged from 1 to 80 m^2 and were at depths between 5.2 and 7.3 m. I opted to conduct the entire study within one study area, because predation rates in the patch-size and edge effects studies (Chapter 3) varied greatly depending upon site.

4.3.2 Habitat Analysis

SCUBA divers videotaped 18 eelgrass patches (1-80 m^2) between August 16 and September 27, 2000, at Mistaken Cove (P3 in Chapter 3), Newman Sound, using an underwater video camera. Because most patches were larger than the field of view of the video camera, I constructed an 8 m^2 grid (Figure 4.1) to act as a reference point and to prevent duplication in recording portions of the patch. The grid was also necessary to apply scale to the video footage.

The grid was constructed of two pieces of ABS (acrylonitrile-butadiene-styrene) piping (2m long and 9 cm in diameter) and three segments of yellow polypropylene rope (4m long and 0.95 cm wide). The ropes were tied through holes drilled in the ABS pipes, creating 2-1m x 4m 'lanes'. Three pieces of aluminum carpet edging (2 m long and 4 cm wide) were used as spreader bars at 1 m intervals on the rope to maintain the shape of the lanes. For the grid to sink, each ABS pipe and each spreader bar was weighted with approximately 680 grams of symmetrically placed lead weights. Each section of rope was marked at 0.25 m intervals with green and orange flagging tape to give finer scale and additional reference to the video footage. As it was designed, the grid could be rolled up underwater and carried to the next patch, making it manageable for divers.

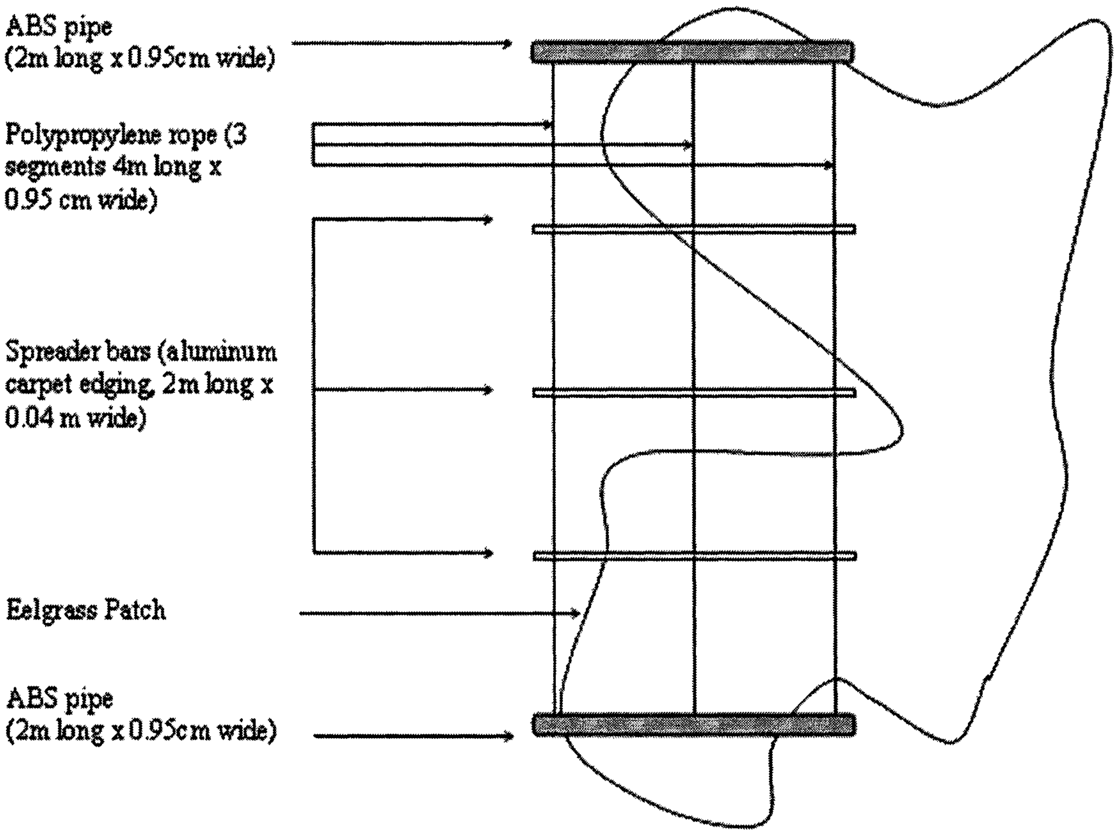

Figure 4.1. SCUBA divers used a 2.0 x 4.0 m grid to add scale and reference to underwater video footage of eelgrass patches. The grid was constructed of 2 ABS pipes and 3 spreader bars, connected by 3 segments of rope. Each rope was marked at 25 cm intervals with flagging tape to add finer scale. Lead weight (680 g) was evenly distributed along each ABS pipe and spreader bar for negative buoyancy. Divers flipped the grid sideways or end-to-end until the entire patch was filmed.

Divers unrolled the grid approximately 4.5 m above the patch and carefully laid on one edge, so as not to disturb the bottom sediment and obstruct visibility. The videographer swam approximately 3.5 m above the grid at a steady pace, ensuring the width of one lane was within the field of view. Each lane was filmed individually. For larger patches (greater than approximately 8 m^2, depending upon shape), the grid was set along the longest edge and was flipped (either sideways or end-to-end) to include the entire patch. For patches larger than 48 m^2, a 10m long baseline (0.95cm wide pink polypropylene rope, weighted by a brick tied to each end) was set at the starting edge. This baseline served as a reference point for divers to line up the grid for each additional flip of the grid. A map of the grid placements was drawn for each patch, so that video footage could be compiled accurately upon analysis. After the last grid of each patch was filmed, the number on the patch marker and a visual estimate of the patch were recorded for future reference. SCUBA divers took visual estimates of the area of each patch to the nearest 1 m^2, knowing that one arms length was approximately 2 m. The smallest patches were filmed first to gain experience in handling the grid.

I analyzed the video by transcribing the presence of eelgrass per 0.0625 m^2 portion of the grid onto graph paper (1 cm^2 grids). This provided a map of the presence or absence of eelgrass per 0.0625 m^2 for each eelgrass patch.

4.3.3 Box-counting

I used a box-counting technique to quantify the perimeter and area at 5 different resolutions. I used grids of box sizes corresponding to 0.0625, 0.25, 1.0, 4.0 and 16.0 m^2. One side of each box corresponded to 0.25, 0.5, 1.0, 2.0 m, and 4.0 m, respectively. The smallest grid size (0.0625 m^2 boxes or 0.25 m sides) is the resolution at which eelgrass presence or absence of eelgrass was transcribed from the video. I laid each grid across the map of each patch and counted the number of boxes that contained eelgrass habitat. To calculate area, I multiplied the number of boxes with eelgrass by the box size. To determine perimeter, I counted the number of box sides around the habitat area and multiplied by length of a side at that resolution. Box-counting was conducted at all five resolutions.

One problem with this technique is that the placement of the grid can greatly affect the number of boxes that contain habitat. Below, I have outlined two methods that I used to deal with this problem:

4.3.3.1 Fixed reference point

I placed a fixed reference point at the bottom, left-hand corner of the map of each patch. I consistently placed the intersection of 4 boxes of the grid directly on to the reference point. The problem with this method was that it did not always measure the minimum area, perimeter or perimeter to area ratio.

4.3.3.2 Minimization

> I also moved each grid to find the minimum area and minimum perimeter possible. This was a more logical method of measurement. When measuring, it was common practice to fit a ruler (resolution) as tightly as possible to the object being measured. This method was also more difficult to conduct. Minimization required several counts to determine the minima, whereas only one count was necessary to do so for the fixed reference point method.

The trouble with this method was that the perimeter corresponding to the minimum area was not the same as that for the minimum perimeter, and vice versa. I assumed that the smallest ratio between perimeter and area (or the minimum (P: A)) would be the most valid measure. Although, determining minimum (P: A) was much more difficult, because it required measuring every possible perimeter and area and then determining which values would produce the lowest ratio. I tried to overcome this problem by demonstrating that minimum P: minimum A and minimum (P: A) were interchangeable. At intermediate resolutions (0.25 and 1.0 m^2), I determined the minimum perimeter to minimum area ratio (minimum P: minimum A). I ranked these from lowest to highest minimum P: minimum A and chose 6 patches that had values that were evenly distributed between the high and low values. Next, I determined the minimum P: A for each of these 6 patches and plotted these as a function of minimum P: minimum A (Figure 4.2 (a, b)). I found that minimum (P: A) is not directly related to minimum P: minimum A, since the slopes for each resolution deviated greatly from the anticipated 1.0. Therefore, I could not use

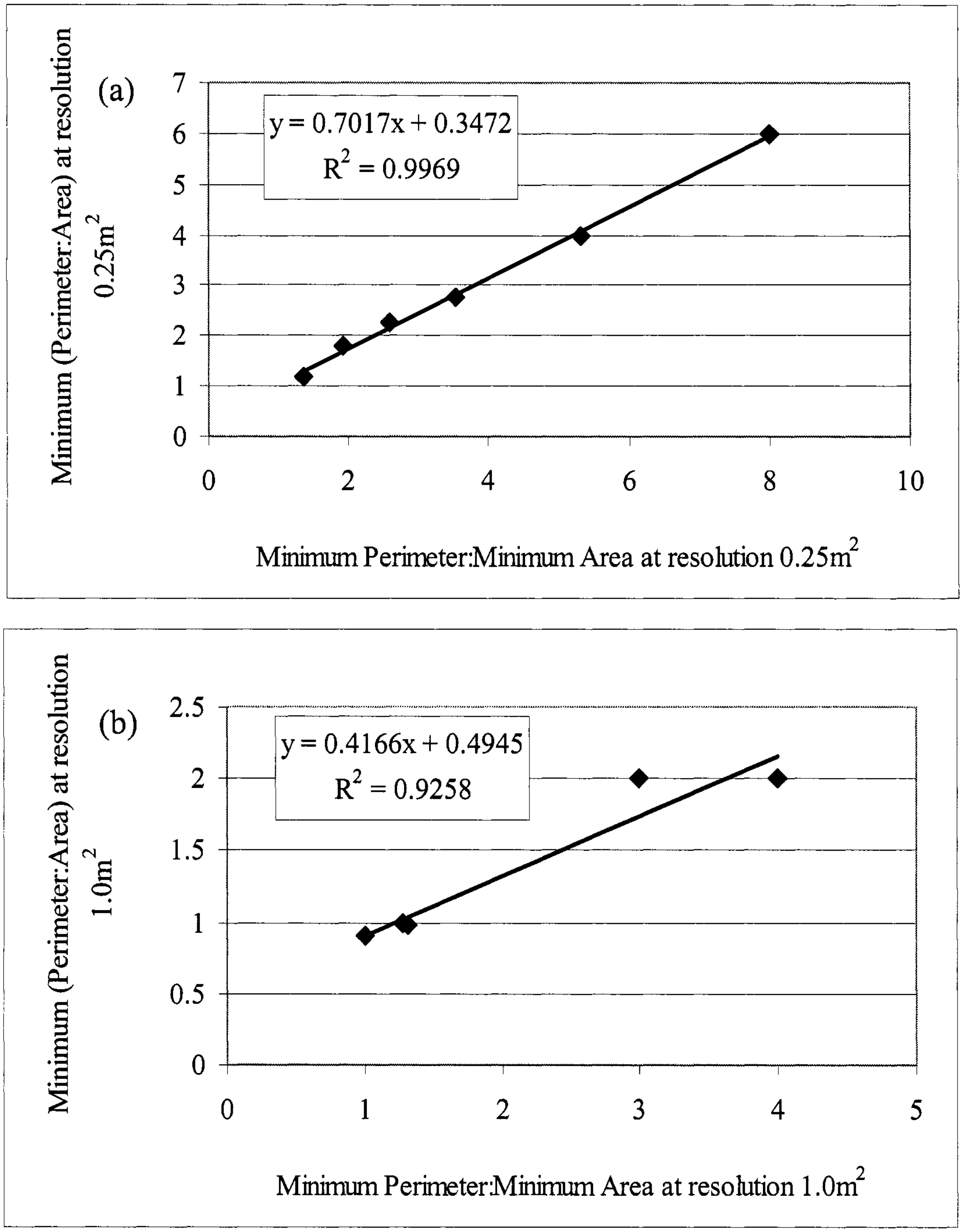

Figure 4.2 (a, b). Relationships between minimum P: minimum A and minimum (P:A) at resolutions of 0.25 (a) and 1.0 m^2 (b). Slopes deviating from 1.0 show that minimum P: minimum A and minimum (P:A) are not interchangeable.

minimum P: minimum A interchangeably with minimum (P: A). Upon reviewing the data necessary for calculating minimum (P: A), I found that these were often the largest possible values for perimeter or area. For this reason, I decided to continue using minimum P: minimum A, since it would be most logical to measure area and perimeter at the smallest rather than the largest possible values.

4.3.4 Calculating Complexity

I calculated the complexity of each patch by using a derivation of the fractal exponent. The fractal exponent is derived from 1- β, where β is the slope of the regression between Ln (Perimeter/Area) and Ln Resolution or box size (m^2). I calculated fractals for each patch with data from each of the two box counting techniques. Exponents ranged from 1.21 to 1.48 and 1.25 to 1.44 using the fixed and minimization box counting methods, respectively. Higher fractal values indicate patches with more edge per unit area.

4.3.5 Tethering

When patch filming was completed, I conducted 8 tether sets at each of the 18 patches October 6-25, 2000. For tethering details, see Methods and Results at Mistaken Cove (P3), 2000, in Chapter 3.

4.4 Results

Using linear regression analysis, I found that the odds of survival of a tethered fish was independent of fractal exponent of patches ($p = 0.26$; $R^2 = 0.058$). Furthermore, there was no relationship between survival and area or perimeter derived from box-counting at any of the 5 resolutions (Appendix B). I also examined the relationship between predation and P: A – another way of assessing perimeter dimension - and found no correlation (Appendix B). These results are inconsistent with the patch-size study results from Chapter 3, which suggested that predation corresponds with visually estimated areas (Figure 3.4 (h)) and that the amount of edge is likely an important factor.

To determine the relevance of box-counting assessments, I compared visually-estimated areas to those from the box-counting technique and found that areas derived from minimization box-counts were correlated with visually estimated areas (Appendix C). Overall, the best relationship found was between visual estimate and box-counting using at the 4 m^2 scale. The measurement calculated at a resolution of 4 m^2 (i.e. 2 m on a side) is most likely consistent with the visual estimate, because that is the approximate "resolution" at which the visual estimates were conducted. Divers estimated patch area by counting the number of arm's-lengths (which were approximately 2 m) for the width and length of the patch. Regarding the lack of relationship between fractal and predation risk, I determined that patch depth was not a confounding factor due to its lack of correlation with fractal exponent (minimization: $p = 0.96$ and $R^2 = 0.0003$; fixed: $p = 0.95$ and $R^2 = 0.001$).

Despite the methodological discrepancies outlined in section 4.2.3, fractal exponents derived from the minimization and fixed box-counting techniques were statistically similar to each other ($p < 0.001$). Although, fractal exponents from the fixed method were consistently greater that those estimated with the minimization technique (fixed = 1.0209*(minimization) - 0.0014, $R^2 = 0.76$). I also found that fractal dimension increased with visually estimated patch area (for minimization, area = 0.0015*(fractal exponent) + 1.30, $p = 0.002$, $R^2 = 0.335$; for fixed, area = 0.0015*(fractal exponent) + 1.33, $p = 0.01$, $R^2 = 0.256$). The correlation between patch area and fractal exponent indicates one of two things: a). that larger patches are more convoluted or b). that my methods of fractal analysis may be incorrectly quantifying habitat structural complexity for a given range of patch sizes.

4.5 Discussion

Contrary to my hypothesis, predation did not correspond to the fractal exponent of individual eelgrass patches. I attribute this to one of two reasons: spatial scale or technique. It is possible that the correlation between patch shape and predation risk is not apparent at the scales of individual patches. Habitat geometry may be linked to predation at the scale of an entire cove or segment of coastline. Work by Ings et al. (2004) and Wells (2002) has demonstrated that density of age-0 cod corresponds with the fractal dimension of eelgrass at spatial scales of 1,500 m^2 and 880 m^2, respectively. Therefore, it is possible that predator densities may follow the same trend. However, I showed in

Chapter 3 that predation correlated with patch edge and area at these scales, demonstrating that predators associated with individual patches at this scale. This observation leads me to believe that measurement scale may not be the reason for the lack of association between predation and complexity.

The correlation between patch shape and predation may not be apparent because of the habitat analysis that I used. First, the presence-absence nature of the transcription process (from video to eelgrass map) is commonly used but not extremely accurate. I believe that it would be better to consider eelgrass to be present per 0.0625 m^2 grid only if it covers >50% of the box. Therefore, patches consisting of a tuft of blades of eelgrass would not be calculated as an area of 0.0625 m^2 and as areas of 0.25, 1.0, 4.0 and 16.0 m^2 with each coarser resolution. Second, within a given patch, I excluded all barren, non-eelgrass 'holes' from the calculated area. I also included the perimeter around these holes as part of the total perimeter. The importance of such holes and corridors with respect to predator and prey movement has not yet been quantified or even evaluated in aquatic species, although there is considerable evidence that such gaps are important in terrestrial environments (Tewksbury et al. 2002). Once the significance of these holes is determined, they could be mathematically weighted depending on importance of size and position within a patch. Until such research is conducted, it would be preferable to only include holes that are contiguous or attach to the edge of the patch, thereby providing more of a corridor than just a barren area. The results from this study imply that holes may be insignificant. I found that the visually estimated areas corresponded with predation, but areas calculated from box counting did not. When visual estimates were taken, they were approximated to the nearest 1 m^2. This means that holes smaller than 1 m^2 were included as eelgrass area. This finding suggests that area and perimeter should encompass the entire patch and holes should be ignored. Lastly, the coarsest resolution should only have been as large as the smallest patch. According to my method, patches 1 m^2 in area scaled up to 4.0 and 16.0 m^2, at those resolutions. It would be more accurate to only use resolutions that the smallest patch fills entirely. As I have calculated them, larger patches have more correctly estimated fractals. This also may explain the correlation between fractal exponent and visually estimated area. The smallest patches are appearing to have less edge per unit area, because they are completely encompassed within one box at some grid resolutions, whereas the largest patches are being more accurately estimated.

4.6 Conclusion

In conclusion, the issues surrounding the methodology may mask the link between predation and patch complexity. The best attempt to resolve some of these issues may be the use of digital spatial analysis. Computation of habitat complexity or fractal dimension could be facilitated by the use of remote sensing or simple integration of habitat data into digital maps. Electronic computation could exponentially increase the types and repetitions of spatial analyses conducted. For example, Appleby (1996) suggests using a randomization placement of the box-counting grid to obtain more accurate assessment of fractal dimension. Such randomization would not be logistically possible using my methods. Lastly, electronic spatial analysis could include a ‘neighborhood’ analysis, which incorporates the morphology of adjacent or nearby patches. Taking a more landscape-based perspective may help to explain the variability associated with predation at the scale of individual patches.

Chapter Five – Summary and Future Application

The results from this study provide evidence that the relationship between predation risk of young cod and refuge habitat is more complex than a simple linear correlation. I found that increasing the areal extent of refugia is linked to increases in local predation risk until patches exceed a threshold area. I speculate that predation is lowest at the largest patch sizes, because predators may opt to search the edge as opposed to areas near the center, which would reduce predation efficiency. By traveling the edges, predators may not be detecting or may be ignoring tethered prey fish in the center of the patch, where it is more difficult to search. Therefore, prey fish located near the center experience reduced predation risk.

These results have substantial implications with respect to the management of Atlantic cod populations. As previously stated, juveniles should be considered an integral component in recruitment models. To date, few attempts have been made to assess predation-related mortality in juveniles. Attempts to understand predation risk at this stage include small-scale, laboratory estimates of refuge preference in the presence/absence of a predator and predator latency periods in these habitats (Gotceitas et al. 1995, Gotceitas et al. 1997) as well as relative predator-prey ratios in preferred and non-preferred habitats (R.S. Gregory, unpublished data, 2000, Laurel et al. 2003) . However, managers have not yet successfully integrated the predator-prey, prey-habitat and predator-habitat components into a single ecosystem model.

My research provides essential information concerning the latter component. I have established that predation risk depends on the spatial configuration of eelgrass patches, as opposed to simply the areal extent of coverage, and that a comprehensive quantification of edge effects is important to future mortality estimates. In order to do this, predation with respect to eelgrass configuration must be examined across multiple scales in time and space; my results merely reflect dynamics occurring at the scale of individual patches.

One approach is to examine predation events with respect to fractal dimension of eelgrass at the scale of coves, bays and even regions. Recent developments in Geographical Information Systems (GIS) and the availability of digital datasets readily allow for the spatial analysis of landscape patterns at broad-scales. The temporal factor is also important considering the notable variability I recorded in daily predation as well as seasonal rises and falls in predation rate. My work focused on predation shortly after settlement occurred in coastal Newfoundland. Because young cod (and their predators) move into deeper water as winter approaches, it is possible that predatory response to edge effects in eelgrass is specific to the early post-settlement period. However, it may be equally valid to presume that predators are affected by the spatial configuration of deeper water refugia during the winter and spring. Based on the variability of predation noted within the relatively narrow season/region that I examined, knowledge of the scaling properties of predation across a broader time-space continuum will surely lead to more accurate assessment of mortality in young cod.

My research can be beneficial to decision-analysis site ranking when managing fish stocks and fish habitat. For instance, coastal nurseries comprised of larger patches, and potentially lower predation, would rank higher than those with many small, discrete patches with higher predation regarding designation of conservation habitats or closed fishing zones. Knowledge of predation relative to patch structure would also be useful when selecting sites to quantify overall predation-related mortality in young cod. Selecting sites with a broad range of patch structures increases the probability of selecting sites with a broad range of predation rates, which would lead to a more accurate assessment of predation mortality for those sites.

REFERENCES

Anderson, J.T., and E.L. Dalley. 1997. Spawning and year-class strength of northern cod (*Gadus morhua*) as measured by pelagic juvenile cod surveys. Canadian Journal of Fisheries and Aquatic Sciences 54(supplement 1): 158-167.

Anderson, J.A., and R. S. Gregory. 1999. Factors regulating survival of northern cod (NAFO 2J3KL) during their first three years of life. ICES Journal of Marine Science 56:1-11.

Andren, H. 1995. Effects of landscape composition on predation rates at habitat edges. In L. Hansson, L. Fahrig, and G. Merriam, eds. Mosaic Landscapes and Ecological Processes. Chapman and Hall. London, England. pp. 225-255.

Andren, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology 69(2):544-547.

Appleby, S. 1996. Multifractal characterization of the distribution pattern of the human population. Geographical Analysis 28: 147-160.

Aronson, R.B., and K.L. Heck Jr. 1995. Tethering experiments and hypothesis testing in ecology. Marine Ecology Progress Series 121: 307-309.

Asthorsson, O.S., A Gislason, and A. Gudmundsdottir. 1994. Distribution, abundance and length of pelagic juvenile cod in Icelandic waters in relation to environmental conditions. ICES Scientific Symposium 198: 529-541.

Balon, E.K. 1975. Terminology of intervals in fish development. Journal of the Fisheries Research Board of Canada 32, 1663-1670.

Bax, N.J. 1998. The significance and prediction of predation in marine fisheries. ICES Journal of Marine Science, 55, 6, 997-1030.

Beck, M. W. 2000. Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. Journal of Experimental Marine Biology and Ecology 249:29-49.

Benoit, H.P., P. Pepin, and J.A. Brown. 2000. Patterns of metamorphic age and length in marine fishes, from individuals to taxa. Canadian Journal of Fisheries and Aquatic Sciences 57: 856- 869.

Bjornstad, O.N., J. Fromentin, N. C. Stenseth, and J. Gjosaeter. 1999. A new test for density-dependent survival: the case of coastal cod populations. Ecology 80(4): 1278-1288.

Bogstad, B., G.R. Lilly, S. Mehl, O.K. Palsson, and G. Stefansson. 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland). ICES Marine Science Symposium. 198:576-599.

Bolz, G.R., and R.G. Lough. 1988. Growth through the first six months of Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, based on daily otolith increments. Fishery Bulletin U.S. 86, 223-235.

Borg, A., L. Pihl, and H. Wennhage. 1997. Habitat choice by juvenile cod (*Gadus morhua* L.) on sandy soft bottoms with different vegetation types. Hergolander Meresuntersuchungen 51: 197-212.

Bottcher, U., R. Oeberst, and B. Mieske. 1998. Daily vertical migration patterns of Baltic 0-group cod. ICES CM 1998/J:9.

Bowman, R.E. 1981. Food of ten species of Northwest Atlantic juvenile groundfish. Fishery Bulletin 79(1):220-226.

Campana, S.E., K.T. Frank, P.C.F. Hurley, P.A. Koeller, F.H. Page, and P.C. Smith. 1989. Survival and abundance of young Atlantic cod (*Gadus morhua*) and haddock (Melanogrammus aeglefinus) as indicators of year-class strength. Canadian Journal of Fisheries and Aquatic Sciences 46(supplement 1): 171-182.

Carr, M.H. 1994. Effects of maroalgal dynamics on recruitment of temperate reef fish. Ecology 75: 1320 - 1333.

Clark, D.S., and J.M. Green. 1989. Activity and movement patterns of juvenile Atlantic cod, *Gadus morhua*, in Conception Bay, Newfoundland, as determined by sonic telemetry. Canadian Journal of Zoology 68: 1434-1442.

Cooper, W.E., and L.B. Crowder. 1979. Patterns of predation in simple and complex environments. Predator-Prey Systems in Fisheries Management. R.H. Stroud and H. Clepper, eds. Sports Fishing Institute, Washington, D.C., U.S.A. pp 257-267.

Cowen, R.K. 1991. Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher*. Marine Ecology Progress Series 69:9-15.

Curran, M., and K. Able. 1998. The value of tethering fishes (winter flounder and tautog) as a tool for assessing predation rates. Marine Ecology Progress Series 163:45-51.

Cushing, D. H. 1975. Marine Ecology and Fisheries. Cambridge University Press, Cambridge, England. pp 278.

Dalley, E. L., and J.T. Anderson. 1997. Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 54(supplement 1): 168-176.

Danilowicz, B. and P. Sale. 1999. Relative intensity of predation of the French grunt, *Haemulaon flavolineatum*, during diurnal, dusk, and nocturnal periods on a coral reef. Marine Biology 133:337-343.

Delong, A.K. and J.S. Collie. 2004. Defining Essential Fish Habitat: A Model-Based Approach. Rhode Island Sea Grant, Narragansett, R.I. 4pp.

Donovan, T.M., P.W. Jones, E.M. Annand, and F.R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology 78(7):2064-2075.

Eggleston, D.B., L.L. Etherington, and W.E. Elis. 1998. Organism response to habitat patchiness: species and habitat recruitment of decapod crustaceans. Journal of Experimental Marine Biology and Ecology 223:111-132.

Elliott, J.K., and W.C. Leggett. 1998. Larval condition and vulnerability to predation: an analysis based on mixed-prey experiments. Canadian Journal of Fisheries and Aquatic Sciences 55: 626–630.

Fagan, W. F., R.S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. The American Naturalist 153:165-182.

Fraser, S., V. Gotceitas, and J.A. Brown. 1996. Interactions between age classes of Atlantic cod and their distribution among bottom substrates. Canadian Journal of Fisheries and Aquatic Sciences 53:305-314.

Fromentin, J.M., N.C. Stenseth, J. Gjosaeter, O.N. Bjornstad, W. Falck, and T. Johannessen. 1997. Spatial patterns of the temporal dynamics of three gadoid species along the Norwegian Skagerrak Coast. Marine Ecology Progress Series 155: 209-222.

Garrison, L.P., W. Michaels, J.S. Link, and M.J. Fogarty. 2000. Predation risk on larval gadids by pelagic fish in the Georges Bank ecosystem. I. Spatial overlap associated with hydrographic features. Canadian Journal of Fisheries and Aquatic Sciences 57: 2455-2469.

Glass, N. R. 1971 Computer analysis of predation energetics in the largemouth bass. In B.C. Patten, ed. Systems Analysis and Simulation Ecology, Volume 1. Academic Press, New York. pp. 325-363.

Goddard, S.V., M.H. Kao, and G.L. Fletcher. 1992. Antifreeze production, freeze resistance, and overwintering of juvenile northern Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 49(30): 516-522.

Godo, O., J. Gjosaeter, K. Sunnana, and O. Dragesund. 1989. Spatial distribution of 0-group gadids off mid-Norway. Rapports et Proces-verbaux des Reunions du Conseil International pour l'Exploration de la Mer 191, 273-280.

Gotceitas, V., and J.A. Brown. 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologia 93: 31-37.

Gotceitas, V., S. Fraser, and J.A. Brown. 1995. Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Marine Biology 123:421-430.

Gotceitas, V., S. Fraser, and J.A. Brown. 1997. Use of eelgrass beds *(Zostera marina)* by juvenile Atlantic cod *(Gadus morhua)*. Canadian Journal of Fisheries and Aquatic Sciences 54:1306-1319.

Grant, S., and J.A. Brown. 1998a. Diel foraging cycles and interactions among juvenile Atlantic cod (*Gadus morhua*) at a nearshore site in Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 55, 1307-1316.

Grant, S., and J.A. Brown. 1998b. Nearshore settlement and localized populations of age-0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 55: 1317-1327.

Gregory, R.S., and J.T. Anderson. 1997. Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Marine Ecology Progress Series 146: 9-20.

Gregory, R.S., and C.D. Levings. 1998. Turbidity reduces predation on migrating juvenile pacific salmon. Transactions of the American Fisheries Society 127:275-285.

Gregory, R.S., B.J. Laurel, D.W. Ings, and D.C. Schneider. 2002. Relative strength of the 2000 year-class, from nearshore surveys of demersal age 0 Atlantic cod in 3KL and in Newman Sound, Bonavista Bay. Canadian Science Advisory Secretariat Proceedings Series 2002/087.

Hancock, J. 2000. Along shore movement of juvenile cod (*Gadus* spp.) determined by mark-recapture. Honor's thesis. Memorial University of Newfoundland, St. John's.

Harden-Jones, F.D. 1968. Fish migration. London, Edward Arnold Ltd., 325 p.

Hawkins, A.D., N.M. Soofiani, and G.W. Smith. 1985. Growth and feeding of juvenile cod (*Gadus morhua* L.). Journal du Conseil International pour l'Exploration de la Mer 42:11-32.

Heck, K.L. Jr., and T.A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. Journal of Experimental Marine Ecology 53: 125-134.

Helfman, G.S. 1986. Fish behaviour by day, night and twilight. In T.J. Pitcher, ed. Behaviour of teleost fishes. Second edition. Chapman and Hall, New York, N.Y. pp. 285-305.

Helle, K., B. Bogstad, C.T. Marshall, K. Michalsen, G. Otteresen, and M. Pennington. 2000. An evaluation of recruitment indices for Arcto-Norwegian cod (*Gadus morhua* L.). Fisheries Research 48 (1): 55-67.

Hobbs, E.R. 1988. Species richness of urban forest patches and implications for urban landscape diversity. Landscape Ecology 1(3): 141-152

Hop, H., J. Gjoesaeter, and D.S. Danielssen. 1994. Dietary composition of sympatric juvenile cod, *Gadus morhua* L., and juvenile whiting, *Merlangius merlangus* L., in a fjord of southern Norway. An International Symposium. Sea ranching of cod and other marine fish species. Aquaculture and Fisheries Management 25 (supplement):49-64

Hunter, J.R.1984. Inferences regarding predators on the early life stages of cod and other fishes. In E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal, eds. The Propagation of Cod *Gadus morhua* L. Flodevigen Rapportser 1: 533-562.

Hussey, K., M.A. St. John, and U. Bottcher. 1997.Food resource utilization by juvenile Baltic cod *Gadus morhua*: a mechanism potentially influencing recruitment success at the demersal juvenile stage? Marine Ecology Progress Series 155: 199-208.

Ings, D.W., D.C. Schneider, R.S. Gregory, and V. Gotceitas. 2004. Density of small fish depends on coastline complexity and local habitat structure. Marine Ecology Progress Series 00:000-000. (In revision)

International Council for the Exploration of the Sea. 2003. Request from the European Commission regarding recovery plans and management measures for cod. 2003. ICES Cooperative Research Report, 261: 965-975. Report of The ICES Advisory Committee on Fishery Management, 2003.

Irlandi, E.A. 1997. Seagrass patch size and survivorship of an infaunal bivalve. OIKOS 78:511-518.

Jackson, G.A., and R.R. Strathmann. 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development. The American Naturalist 118: 16-26.

Kao, M.H., and G.L. Fletcher. 1988. Juvenile Atlantic cod (*Gadus morhua*) can be more freeze resistant than adults. Canadian Journal of Fisheries and Aquatic Sciences 45(5): 902-905.

Keats, D.W. 1990. A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern Newfoundland. Journal of Experimental Marine Biology and Ecology 139: 167-173.

Keats, D.W., D.H. Steele, and G.R. South. 1987. The role of fleshy macroalgae in the ecology of juvenile cod (*Gadus morhua* L.) in inshore waters off eastern Newfoundland. Canadian Journal of Zoology 65:49-53.

Kenkel, N.C., and D.J. Walker. 1996. Fractals in the biological sciences. Coenoses 11: 77-100.

Laurel, B.J., R.S. Gregory, and J.A. Brown. 2003a. Settlement and distribution of age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following large-scale habitat manipulation. Marine Ecology Progress Series 262: 241-252.

Laurel, B.J., R.S. Gregory, and J.A. Brown. 2003b. Predator distribution and habitat patch area determine predation rates on Age-0 juvenile cod *Gadus* spp. Marine Ecology Progress Series 251: 245-254.

Laurel, B.J., R.S. Gregory, J.A. Brown, J. K. Hancock, and D.C. Schneider. 2004. Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. Marine Ecology Progress Series 272: 257-270.

Leis, J.M. 1991. Vertical distribution of fish larvae in the Great Barrier Reef Lagoon, Australia. Marine Biology 109: 157-166.

Leis, J.M. and B.M. Carson-Ewart. 1998. Complex behaviour by coral reef fish larvae in open-water and near-reef pelagic environments. Environmental Biology of Fishes 53: 259-266.

Leising, A.W. and P.J.S. Franks. 1999. Larval Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) growth on Georges Bank: a model with temperature, prey size, and turbulence forcing. Canadian Journal of Fisheries and Aquatic Sciences 56:25-36.

Levin, P.S. 1994. Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. Environmental Biology of Fish 40: 271-281.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73(6):1943-1967.

Lima, S.L. and L.M. Dill. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Linehan, J.E., R.S. Gregory, and D.C. Schneider. 2001. Predation risk of age-0 cod relative to depth and substrate in coastal waters. Journal of Experimental Marine Biology and Ecology 263:25-44.

Lindholm, J.B., P.J. Auster, and L.S. Kaufman. 1999. Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua.* Marine Ecology Progress Series 180:247-255.

Lomond, T., D.C. Schneider and D.A. Methven. 1998. Transition from pelagic to benthic prey for age group 0-1 Atlantic cod, *Gadus morhua*. Fishery Bulletin 96(4): 908-911.

Lough, R.G., C.V. Page, D.C. Potter, P.J. Auditore, G.R. Bolz, J.D. Neilson, and R.I. Perry. 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on the eastern Georges Bank. Marine Ecology Progress Series 56: 1-12.

Lough, R.G., E.M. Caladrone, T.K. Rotunno, E.A. Broughton, B.R. Burns, and L.J. Buckley. 1996. Vertical distribution of cod and haddock egg and larvae, feeding and condition in stratified and mixed waters on southern Georges Bank, May 1992. Deep-Sea Research. Part II Top. Stud. Oceanography. 43: 1875-904.

Macdonald, J.S., M.J. Dadswell, R.G. Appy, G.D. Melvin, and D.A. Methven. 1984. Fishes, fish assemblages and their seasonal movements in lower Bay of Fundy and Passamaquoddy Bay, Canada. Fishery Bulletin. U.S. 82: 121-139.

Manly, B. F. J. 1991. Randomization and Monte-Carlo Methods in Biology. London: Chapman & Hall.

Marliave, J.B. 1977. Substratum preferences of settling larvae of marine fishes reared in the laboratory. Journal of Experimental Marine Biology and Ecology 153: 195-205.

Mattila, J. 1992. The effect of habitat complexity on predation efficiency of perch *Perca fuviatilis* L. and ruffe *Gymnocephalus cernuus* (L.). Journal of Experimental Marine Biology and Ecology 157: 55-67.

Methven, DA, and C. Bajdik. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern. Canadian Journal of Fisheries and Aquatic Sciences 51(1): 78-90.

Methven, D.A., and C. McGowan. 1998. Distinguishing small juvenile Atlantic cod (*Gadus morhua*) from Greenland cod (*Gadus ogac*) by comparing meristic characters and discriminant function analyses of morphometric data. Canadian Journal of Zoology 76(6): 1054-1062.

Methven, D.A., and D.C. Schneider. 1998. Gear-independent patterns of variation in catch of juvenile Atlantic cod (*Gadus morhua*) in coastal habitats. Canadian Journal of Fisheries and Aquatic Sciences 55:1430-1442.

Modin, J., and L. Pihl. 1996. Small-scale dispersal of 0-group plaice (*Pleuronectes platessa* L.) and flounder (*Plactichthys flesus* L.) in a shallow Swedish bay. Journal of Fish Biology 49: 1070-1085.

Moen, J., and B.G. Jonsson. 2003. Edge Effects on Liverworts and Lichens in Forest Patches in a Mosaic of Boreal Forest and Wetland. The Journal of the Society for Conservation Biology 17(2):380-388.

Nelson, W.G., and E. Bonsdorff. 1990. Fish predation and habitat complexity: are complexity thresholds real? Journal of Experimental Marine Biology and Ecology 141:183-194.

Nikora, V.I., C.P. Pearson, and U. Shankar. 1999. Scaling properties in landscape patterns: a New Zealand experience. Landscape Ecology 14:17-33.

Office of Seafood and Office of Regulatory Affairs, U.S. Food and Drug Administration. 1993-2004. Regulatory Fish Encyclopedia. United Sates Food and Drug Administration website. Available at: http://www.cfsan.fda.gov/~frf/rfe0.html. Accessed March 9, 2004.

Oiestad, V., P.G. Kvenseth, and A. Folkvord. 1985. Mass production of Atlantic cod juveniles *Gadus morhua* in a Norwegian saltwater pond. Transactions of the American Fisheries Society 114: 590-595.

Olsen, S., and A.V. Soldal. 1989. Observations on inshore distribution and behaviour of 0-group northeast Arctic cod. Rapports et Proces-verbaux des Reunions du Conseil International pour l'Exploration de la Mer 191: 296-302.

Pedersen, T., Eliassen, J. E., Eilertsen, H. C., Tande, K. S. and Olsen, R. E. (1989). Feeding, growth, lipid composition and survival of larval cod (*Gadus morhua* L.) in relation to environmental conditions in an enclosure at 70 ° in Northern Norway. Rapports et Proces-verbaux des Reunions du Conseil International pour l'Exploration de la Mer 191, 409–420.

Pedersen, T. and I.B. Falk-Petersen. 1992. Morphological changes during metamorphosis in cod (*Gadus morhua*), with particular reference to the development of the stomach and pyloric caeca. Journal of Fish Biology 41: 449-461.

Pepin, P. and J.A. Helbig. 1997. Distribution and drift of Atlantic cod (*Gadus morhua*) eggs and larvae on the northeast Newfoundland Shelf. Canadian Journal of Fisheries and Aquatic Sciences 54: 670-685.

Perry, R.I., and J.D. Neilson. 1988. Vertical distributions and trophic interactions of age-0 Atlantic cod and haddock in mixed and stratified waters of Georges Bank. Marine Ecology Progress Series 49: 199-214.

Pihl, L. 1982. Food intake of young cod and flounder in a shallow bay on the Swedish west coast. Netherlands Journal of Sea Research 15: 419-432.

Pitcher, T. J., and J. K. Parrish. 1993. Functions of shoaling behaviour in teleosts. In T. J. Pitcher, ed. Behaviour of teleost fishes. Second edition. Chapman and Hall, London, UK. pp. 363-439.

Post, J.R., E.A. Parkinson, and N.T. Johnson. 1998. Spatial and temporal variation in risk to piscivory of age-0 rainbow trout: patterns and population level consequences. Transactions of the American Fisheries Society 127:932-942.

Preen, A.R. W.J. Lee Long, and R.G. Coles. 1999. Flood and cyclone related loss, and partial recovery, of more than 1000 km^2 of seagrass in Hervey Bay, Queensland, Australia. Aquatic Botany 52 (1-2): 3-17.

Riley, J. D., and W.G. Parnell.1984. The distribution of young cod. In The Propagation of Cod (*Gadus morhua* L.). E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal, eds. Flodevigen Rapportser 1: 563–580.

Robb, A.P., and J.R.G. Hislop. 1980. The food of five gadoid species during the pelagic O-group phase in the northern North Sea. Journal of Fish Biology 16:199-217.

Robertson, D.R., S.E. Swearer, K. Kaufmann, and E Brothers. 1999. Settlement vs. environmental dynamics in a pelagic-spawning reef fish at Caribbean Panama. Ecological Monographs 69: 195 –218.

Salvanes, A.G.V., D.L. Aksnes, and J. Giske. 1992. A simulation model for evaluating the potential production of cod in a west Norwegian fjord. Nordic workshop on predation processes and predation models. Seminar at Stykkishomur, 7-11 September 1992., Nordisk Ministerraad, Copenhagen (Denmark), 1993, pp. 151-155.

Salvanes, A.G.V., J. Giske and J.T. Nordeide. 1994. Life-history approach to habitat shifts for coastal cod, *Gadus morhua* L. Aquaculture and Fisheries Management 25 (supplement 1): 215-228.

Schneider, D.C., E.L. Dalley, and J.T. Anderson. 1997. A combined recruitment index for demersal juvenile cod in NAFO divisions 3K and 3L. NAFO Scientific Council Studies 29:23-29.

Scott, W.B., and M.G. Scott. 1988. Atlantic Fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences 219:731pp.

Sinclair, M. 1988. Marine Populations: an Essay on Population Regulation and Speciation. University of Washington Press, Seattle, 252 pp.

Sissenwine, M. P., E.B. Cohen, and M.D. Grosslein.1984. Structure of the Georges Bank ecosystem. Rapports et Proces-verbaux des Reunions du Conseil International pour l'Exploration de la Mer 183:243-254.

Sogard, S. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60(3): 1129-1157.

Sovada, M.A., M.C. Zicus, R.J. Greenwood, D.P. Rave, W.E. Newton, R.O. Woodward, and J.A. Beiser. 2000. Relationships of habitat patch size to predator community and survival of duck nests. Journal of Wildlife Management 64(3): 820-831.

Stamps, J.A., M. Buechner, and V.V. Krishnan. 1987. The effects of habitat geometry on territorial defense costs: intruder pressure in bounded habitats. American Zoology 27: 307-325.

Stottrup J.G., J.R. Nielsen, C. Krog,, and K. Rasmussen. 1994. Results on the extensive production of North Sea cod, *Gadus morhua* L., and their growth and distribution subsequent to release in the Limfjord, Denmark. Aquatic Fisheries Management 25(supplement 1): 143-160.

Suthers, I.M., and K.T. Frank. 1989. Inter-annual distributions of larval and pelagic juvenile cod (*Gadus morhua*) in southwestern Nova Scotia determined with two different gear types. Canadian Journal of Fisheries and Aquatic Sciences 46: 591-602.

Suthers, I.M., K.T. Frank, and S.E. Campana. 1989. Spatial comparison of recent growth in postlarval Atlantic cod (*Gadus morhua*) off Southwestern Nova Scotia: Inferior growth in a presumed nursery area. Canadian Journal of Fisheries and Aquatic Sciences 46: 113-124.

Swain, D.P., and A.F. Sinclair. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic science 57:1321-1325.

Sweatman, H. 1988. Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. Journal of Experimental Marine Biology and Ecology 124: 163-174.

Tewksbury, J.J., S.J. Hejl, and T.E. Martin. 1998. Breeding Productivity Does Not Decline with Increasing Fragmentation in a Western Landscape Ecology 79(8):2890-2903.

Tewksbury, J.J., D.J. Levey, N.M, Haddad, S. Sargent, J.L. Orrock, A. Weldon, B.J.Danielson, J. Brinkerhoff, E.I. Damschen, and P. Townsend. 2002. Corridors affect plants, animals and their interactions in fragmented landscapes. Proceedings of the National Academy of Sciences of the United States of America 99: 12923-12926.

Tsou, T. and J. S. Collie. 2001. Estimating predation mortality in the Georges Bank fish community. Canadian Journal of Fisheries and Aquatic Sciences 58(5): 908-922.

Tupper, M., and R.G. Boutilier. 1995a. Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. Marine Ecology Progress Series 118: 295-300.

Tupper, M., and R.G. Boutilier. 1995b. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 52: 1834-1841.

Tveite S. 1984. 0-Group cod investigations on the Norwegian Skagerrak coast. In The propagation of cod, *Gadus morhua* L. E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal, eds. Flodevigen Rapportser 1: 581-590.

Victor, B.C. 1986. Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). Canadian Journal of Fisheries and Aquatic Sciences 43:1208-1213.

Wells, N.J. 2002. Scaling eelgrass complexity in Newman Sound, Newfoundland and applications to fish ecology. MSc thesis, Memorial University of Newfoundland, St. John's. 103 pp.

Wennhage, H., and R.N. Gibson. 1998. Influence of food supply and a potential predator (*Crangon crangon*) on settling behaviour of plaice (*Pleuronectes platessa*). Journal of Sea Research 39:103-112.

Werner, E.E., J.F. Gilliam, D. J. Hall, and G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64(6):1540-1548.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393-425.

Werner, F.E., R.I. Perry, R.G. Lough, and C.E. Naimie. 1996. Trophodynamic and advective influences on Georges Bank larval cod and haddock. Deep-Sea Research. Part II. Topical Studies in Oceanography. 43:1793–1822.

Williams, PJ, J.A. Brown, V. Gotceitas, and P. Pepin. 1996. Developmental changes in escape response performance of five species of marine larval fish. Canadian Journal of Fisheries and Aquatic Sciences 53(6): 1246-1253.

Wilson, K.A., K.L. Heck, Jr., and K.W. Able. 1987. Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as refuge. Fishery Bulletin US 85: 53-58.

Wilson, K.A., K.W. Able, and K.L. Heck Jr. 1990. Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence or the importance of macroalgae (*Ulva lactuca*). Marine Ecology Progress Series 58: 243-251.

APPENDICES

Appendix A: P-values for the Edge Effects Study. Results in the text of the thesis were reported based on grouping by period at each site, however, there were no significant results to report based on that grouping. When data were separated by site and period, several treatments proved to have significantly lower predation risk than the edge. Subset 'a' represents data divided into each of the 5 locations, whereas subset 'b' represents data pooled by substrate.

		a). P-values, compared to EDGE				b). P values, compared to EDGE	
Site	**Period**	**Grass10**	**Grass5**	**Mud5**	**Mud10**	**GRASS**	**MUD**
E1	1	0.3904	1	0.6738	0.9999	0.6243	0.1124
	2	0.1645	0.9999	0.0107**	0.0107**	0.0085**	0.0013**
	3	0.7947	0.8702	0.1899	0.072	0.8091	0.0513
	4	0.5845	0.5443	0.9999	0.9999	0.5028	0.9999
E2	1*	1	1	1	1	1	1
	2	0.1058	0.617	0.6542	0.2129	0.4562	0.3315
	3	0.0399**	0.6824	0.3904	1	0.2672	0.6243
	4	0.0394**	0.3946	0.1528	0.0295**	0.0886	0.0345**
Overall		0.1554	0.0816	0.0123**	0.0005**	0.085	0.0001**

* Denotes 100% predation

** Denotes significant p-values

Appendix B: P-values and R^2 values for the relationships between odds of survival and patch area or perimeter derived from box-counting in Chapter 4.

	Area		**Perimeter**		**Perimeter/Area**	
Resolution	**p-value**	**R^2**	**p-value**	**R^2**	**p-value**	**R^2**
0.0625m^2	0.907	0.001	0.733	0.005	0.921	0.000
0.25m^2	0.831	0.002	0.770	0.003	0.252	0.052
1.0m^2	0.801	0.003	0.976	0.000	0.142	0.084
4.0m^2	0.841	0.002	0.883	0.001	0.567	0.013
16.0m^2	0.810	0.002	0.888	0.001	0.980	0.000

Appendix C: P-values, R^2 values and linear regression for the relationships between visually estimated area and area derived from box-counting (minimization) in Chapter 4. Overall, areas measured with at the $4.0m^2$ scale were most similar to those estimated in the field.

Resolution	**p-value**	**R^2**	**Equation**
$0.0625m^2$	3.23E-07	0.686	$y = 0.4345x + 1.436$
$0.25m^2$	4.02E-08	0.737	$y = 0.662x + 1.567$
$1.0m^2$	3.76E-10	0.824	$y = 0.911x + 2.584$
$4.0m^2$	1.51E-10	0.837	$y = 1.030x + 4.629$
$16.0m^2$	5.82E-10	0.817	$y = 1.355x + 14.660$

Appendix D: Raw data from the Patch-Size Study (Chapter 3)

S	p	n	a	tsp	lsl	out	bsl
B	2	11	2	O	94	al	.
B	2	12	12	O	85	al	.
B	2	10	6	O	89	al	.
B	2	9	2	O	90	al	.
B	2	8	20	O	70	al	.
B	2	11	2	O	94	al	.
B	2	12	12	O	85	al	.
B	2	10	6	O	89	al	.
B	2	9	2	O	90	al	.
B	2	8	20	O	70	al	.
B	2	11	2	O	94	al	.
B	2	12	12	O	85	al	.
B	2	10	6	O	89	al	.
B	2	8	20	O	70	al	.
B	2	11	2	O	94	al	.
B	2	10	6	O	89	al	.
B	2	9	2	O	90	al	.
B	2	8	20	O	70	al	.
B	2	11	2	O	94	al	.
B	2	12	12	O	95	al	.
B	2	10	6	O	89	al	.
B	2	12	12	O	94	al	.
B	2	10	6	O	84	al	.
B	2	11	2	O	94	al	.
B	2	12	12	O	94	al	.
B	2	10	6	O	84	al	.
B	2	9	2	O	92	al	.
B	2	11	2	O	94	al	.
B	2	12	12	O	94	al	.
B	2	10	6	O	84	al	.
B	2	9	2	O	92	al	.
B	2	8	20	O	88	al	.
B	2	11	2	O	94	al	.
B	2	12	12	O	94	al	.
B	2	10	6	O	84	al	.
B	2	9	2	O	92	al	.
B	2	8	20	O	88	al	.
B	2	11	2	O	94	al	.
B	2	12	12	O	94	al	.
B	2	10	6	O	84	al	.
B	2	9	2	O	92	al	.
B	2	8	20	O	88	al	.

Abbreviations	
s	site
p	period
n	patch #
a	patch area (m^2)
tsp	tethered animal's SL
lsl	tethered animal's spp.
out	outcome
bsl	predator's SL, if caught

site	
B	Big Brook1999
H	Heffern's 1999
M	Mistaken 2000
T	Mistaken 1999
period	
1	9/13-17/99
2	9/27-30/99
3	10/8-12/99
4	10/13-25/99
5	10/26-28/99
9	10/6 - 11/25/00
tsp	Species of tethered fish
M	*Gadus morhua*
O	*Gadus ogac*
outcome	
al	alive
at	attacked
cu	cunner
fg	tethered fish gone
hg	hook gone
mo	*Gadus morhua*
og	*Gadus ogac*
sc	sculpin

B	2	9	2	O	92	mo	23.0
B	2	8	20	O	88	hg	.
B	2	9	2	O	90	al	.
B	2	12	12	O	85	al	.
B	2	8	20	O	70	al	.
B	2	11	2	O	94	al	.
B	2	9	2	O	92	al	.
B	2	8	20	O	70	al	.
B	2	15	8	O	85	al	.
B	2	14	12	O	96	al	.
B	2	5	6	O	86	al	.
B	2	13	6	O	91	al	.
B	2	3	3	M	71	al	.
B	2	15	8	O	85	al	.
B	2	14	12	O	96	al	.
B	2	5	6	O	86	al	.
B	2	13	6	O	91	al	.
B	2	3	3	M	71	al	.
B	2	15	8	O	85	al	.
B	2	14	12	O	96	al	.
B	2	5	6	O	86	al	.
B	2	13	6	O	91	al	.
B	2	3	3	M	71	al	.
B	2	15	8	O	85	al	.
B	2	14	12	O	96	al	.
B	2	5	6	O	86	al	.
B	2	13	6	O	91	al	.
B	2	15	8	O	85	al	.
B	2	14	12	O	96	al	.
B	2	5	6	O	86	al	.
B	2	13	6	O	91	al	.
B	2	3	3	O	94	al	.
B	2	14	12	O	96	al	.
B	2	13	6	O	91	al	.
B	2	3	3	O	94	al	.
B	2	15	8	O	92	al	.
B	2	14	12	O	96	al	.
B	2	5	6	O	86	al	.
B	2	13	6	O	91	al	.
B	2	3	3	O	94	al	.
B	2	15	8	O	92	al	.
B	2	14	12	O	96	al	.
B	2	5	6	O	86	al	.
B	2	13	6	O	91	al	.
B	2	3	3	O	94	al	.
B	2	15	8	O	92	al	.

B	2	14	12	O	96	al	.
B	2	5	6	O	86	al	.
B	2	13	6	O	91	al	.
B	2	3	3	O	94	al	.
B	2	15	8	O	92	al	.
B	2	14	12	O	96	al	.
B	2	5	6	O	86	al	.
B	2	13	6	O	91	al	.
B	2	3	3	M	71	fg	.
B	2	15	8	O	85	sc	15.5
B	2	3	3	M	71	al	.
B	2	5	6	O	86	al	.
B	2	4	15	O	92	al	.
B	2	6	16	O	90	al	.
B	2	2	1	O	93	al	.
B	2	7	49	O	92	al	.
B	2	6	16	O	94	al	.
B	2	1	16	O	80	al	.
B	2	4	15	O	96	al	.
B	2	2	1	O	93	al	.
B	2	7	49	O	92	al	.
B	2	4	15	O	96	al	.
B	2	2	1	O	93	al	.
B	2	7	49	O	92	al	.
B	2	6	16	O	94	al	.
B	2	1	16	O	80	al	.
B	2	7	49	O	92	al	.
B	2	6	16	O	94	al	.
B	2	4	15	O	96	al	.
B	2	7	49	O	92	al	.
B	2	6	16	O	94	al	.
B	2	1	16	O	92	al	.
B	2	4	15	O	96	al	.
B	2	2	1	O	100	al	.
B	2	7	49	O	92	al	.
B	2	6	16	O	94	al	.
B	2	1	16	O	92	al	.
B	2	4	15	O	92	al	.
B	2	7	49	O	92	al	.
B	2	2	1	O	87	al	.
B	2	7	49	O	92	al	.
B	2	6	16	O	90	al	.
B	2	4	15	O	92	al	.
B	2	2	1	O	87	al	.
B	2	6	16	O	90	al	.
B	2	4	15	O	92	al	.

B	2	2	1	O	87	al	.
B	2	7	49	O	92	al	.
B	2	4	15	O	96	sc	18.0
B	2	1	16	O	80	at	.
B	2	2	1	O	93	at	.
B	2	2	1	O	100	sc	21.0
B	2	6	16	O	94	al	.
B	2	4	15	O	96	al	.
B	2	2	1	O	93	al	.
B	2	1	16	O	80	al	.
B	2	6	16	O	90	al	.
B	4	11	2	M	57	al	.
B	4	12	12	M	66	al	.
B	4	10	6	M	48	al	.
B	4	9	2	M	57	al	.
B	4	8	20	M	62	al	.
B	4	10	6	M	48	al	.
B	4	9	2	M	57	al	.
B	4	8	20	M	73	al	.
B	4	11	2	M	75	al	.
B	4	12	12	M	66	al	.
B	4	10	6	M	61	al	.
B	4	9	2	M	64	al	.
B	4	8	20	M	73	al	.
B	4	9	2	M	64	al	.
B	4	8	20	M	73	al	.
B	4	11	2	M	75	al	.
B	4	10	6	M	59	al	.
B	4	9	2	M	64	al	.
B	4	8	20	M	73	al	.
B	4	11	2	M	75	al	.
B	4	11	2	M	57	mo	24.5
B	4	8	20	M	62	sc	18.0
B	4	12	12	M	66	og	13.0
B	4	12	12	M	66	al	.
B	4	10	6	M	48	al	.
B	4	12	12	M	66	al	.
B	4	10	6	M	59	al	.
B	4	12	12	M	66	al	.
B	4	11	2	M	75	al	.
B	4	11	2	M	75	al	.
B	4	12	12	M	66	al	.
B	4	9	2	M	64	al	.
B	4	8	20	M	73	al	.
B	4	11	2	M	63	al	.
B	4	9	2	M	73	al	.

B	4	10	6	M	60	al	.
B	4	11	2	M	63	al	.
B	4	9	2	M	73	al	.
B	4	12	12	M	66	al	.
B	4	10	6	M	60	al	.
B	4	9	2	M	73	al	.
B	4	12	12	M	66	al	.
B	4	10	6	M	60	al	.
B	4	12	12	M	59	fg	.
B	4	8	20	M	74	fg	.
B	4	8	20	M	73	og	17.5
B	4	8	20	M	75	mo	16.5
B	4	7	49	M	54	al	.
B	4	13	6	M	74	al	.
B	4	5	6	M	57	al	.
B	4	7	49	M	59	al	.
B	4	5	6	M	57	al	.
B	4	7	49	M	59	al	.
B	4	5	6	M	57	al	.
B	4	7	49	M	59	al	.
B	4	13	6	M	74	al	.
B	4	14	12	M	61	al	.
B	4	6	16	M	65	al	.
B	4	13	6	M	74	al	.
B	4	5	6	M	57	al	.
B	4	7	49	M	59	al	.
B	4	6	16	M	65	al	.
B	4	13	6	M	74	al	.
B	4	14	12	M	63	al	.
B	4	5	6	M	57	al	.
B	4	7	49	M	59	al	.
B	4	6	16	M	65	al	.
B	4	13	6	M	74	al	.
B	4	5	6	M	57	al	.
B	4	7	49	M	55	al	.
B	4	6	16	M	65	al	.
B	4	13	6	M	74	al	.
B	4	14	12	M	82	al	.
B	4	5	6	M	57	al	.
B	4	7	49	M	59	al	.
B	4	6	16	M	65	al	.
B	4	13	6	M	74	al	.
B	4	14	12	M	82	al	.
B	4	5	6	M	57	al	.
B	4	6	16	M	63	al	.
B	4	14	12	M	82	al	.

B	4	5	6	M	52	al	.
B	4	6	16	M	67	mo	17.5
B	4	14	12	M	67	og	15.5
B	4	14	12	M	60	hg	.
B	4	14	12	M	63	sc	15.0
B	4	6	16	M	58	sc	18.0
B	4	14	12	M	61	fg	.
B	4	14	12	M	63	sc	20.5
B	4	13	6	M	74	al	.
B	4	5	6	M	57	al	.
B	4	7	49	M	59	al	.
B	4	15	8	M	69	al	.
B	4	3	3	M	73	al	.
B	4	2	1	M	75	al	.
B	4	4	15	M	73	al	.
B	4	1	16	M	61	al	.
B	4	15	8	M	69	al	.
B	4	3	3	M	73	al	.
B	4	2	1	M	75	al	.
B	4	4	15	M	73	al	.
B	4	1	16	M	61	al	.
B	4	15	8	M	69	al	.
B	4	3	3	M	73	al	.
B	4	2	1	M	75	al	.
B	4	4	15	M	73	al	.
B	4	1	16	M	61	al	.
B	4	15	8	M	69	al	.
B	4	3	3	M	73	al	.
B	4	2	1	M	75	al	.
B	4	4	15	M	73	al	.
B	4	1	16	M	61	al	.
B	4	15	8	M	69	al	.
B	4	3	3	M	73	al	.
B	4	2	1	M	75	al	.
B	4	4	15	M	73	al	.
B	4	1	16	M	61	al	.
B	4	15	8	M	69	al	.
B	4	3	3	M	73	al	.
B	4	2	1	M	75	al	.
B	4	4	15	M	73	al	.
B	4	1	16	M	61	al	.
B	4	15	8	M	69	al	.
B	4	3	3	M	73	al	.
B	4	2	1	M	75	al	.
B	4	4	15	M	73	al	.
B	4	1	16	M	61	al	.

B	4	15	8	M	59	al	.
B	4	3	3	M	73	al	.
B	4	15	8	M	59	al	.
B	4	3	3	M	73	al	.
B	4	2	1	M	60	al	.
B	4	4	15	M	54	al	.
B	4	1	16	M	61	al	.
B	4	15	8	M	69	al	.
B	4	3	3	M	73	al	.
B	4	2	1	M	60	al	.
B	4	4	15	M	54	al	.
B	4	1	16	M	61	al	.
B	4	2	1	M	75	sc	16.0
B	4	4	15	M	73	al	.
B	4	1	16	M	61	al	.
B	5	8	20	M	51	al	.
B	5	9	2	M	76	al	.
B	5	10	6	M	52	al	.
B	5	12	12	O	90	al	.
B	5	11	2	M	51	al	.
B	5	8	20	M	51	al	.
B	5	9	2	M	76	al	.
B	5	10	6	M	52	al	.
B	5	12	12	O	90	al	.
B	5	11	2	M	51	al	.
B	5	8	20	M	51	al	.
B	5	9	2	M	76	al	.
B	5	10	6	M	52	al	.
B	5	12	12	O	90	al	.
B	5	11	2	M	51	al	.
B	5	8	20	M	51	al	.
B	5	10	6	M	52	al	.
B	5	12	12	O	90	al	.
B	5	11	2	M	66	al	.
B	5	8	20	M	51	al	.
B	5	9	2	M	76	al	.
B	5	10	6	M	52	al	.
B	5	12	12	O	90	al	.
B	5	11	2	M	66	al	.
B	5	8	20	M	51	al	.
B	5	9	2	M	76	al	.
B	5	10	6	M	52	al	.
B	5	12	12	O	90	al	.
B	5	11	2	M	66	al	.
B	5	9	2	M	76	al	.
B	5	10	6	M	52	al	.

B	5	12	12	O	90	al	.
B	5	11	2	M	66	al	.
B	5	9	2	M	76	al	.
B	5	8	20	M	51	og	16.0
B	5	1	16	M	55	al	.
B	5	4	15	M	58	al	.
B	5	2	1	M	66	al	.
B	5	3	3	M	57	al	.
B	5	15	8	M	57	al	.
B	5	1	16	M	55	al	.
B	5	4	15	M	58	al	.
B	5	2	1	M	66	al	.
B	5	3	3	M	57	al	.
B	5	15	8	M	57	al	.
B	5	1	16	M	55	al	.
B	5	4	15	M	58	al	.
B	5	2	1	M	66	al	.
B	5	3	3	M	57	al	.
B	5	15	8	M	57	al	.
B	5	1	16	M	55	al	.
B	5	4	15	M	58	al	.
B	5	2	1	M	66	al	.
B	5	3	3	M	57	al	.
B	5	15	8	M	57	al	.
B	5	1	16	M	55	al	.
B	5	4	15	M	58	al	.
B	5	3	3	M	57	al	.
B	5	15	8	M	57	al	.
B	5	2	1	M	66	al	.
B	5	3	3	M	57	al	.
B	5	1	16	M	52	al	.
B	5	4	15	M	58	al	.
B	5	2	1	M	66	al	.
B	5	3	3	M	57	al	.
B	5	15	8	M	57	al	.
B	5	1	16	M	52	al	.
B	5	4	15	M	58	al	.
B	5	2	1	M	57	al	.
B	5	3	3	M	57	al	.
B	5	15	8	M	57	al	.
B	5	1	16	M	52	al	.
B	5	4	15	M	58	al	.
B	5	2	1	M	57	al	.
B	5	3	3	M	57	al	.
B	5	15	8	M	57	al	.
B	5	1	16	M	52	al	.

B	5	4	15	M	63	al	.
B	5	2	1	M	57	al	.
B	5	3	3	M	68	al	.
B	5	15	8	M	57	al	.
B	5	2	1	M	66	al	.
B	5	1	16	M	52	al	.
B	5	4	15	M	58	al	.
B	5	15	8	M	57	al	.
B	5	9	2	M	56	al	.
B	5	10	6	M	63	al	.
B	5	12	12	M	80	al	.
B	5	11	2	M	71	al	.
B	5	8	20	M	67	al	.
B	5	9	2	M	56	al	.
B	5	10	6	M	63	al	.
B	5	12	12	M	80	al	.
B	5	11	2	M	71	al	.
B	5	9	2	M	56	al	.
B	5	11	2	M	71	al	.
B	5	8	20	M	68	sc	18.0
B	5	10	6	M	63	sc	30.0
B	5	12	12	M	80	sc	20.0
B	5	8	20	M	67	al	.
B	5	7	49	M	71	al	.
B	5	14	12	O	97	al	.
B	5	5	6	M	67	al	.
B	5	7	49	M	71	al	.
B	5	6	16	M	68	al	.
B	5	13	6	O	94	al	.
B	5	14	12	O	97	al	.
B	5	7	49	M	71	al	.
B	5	13	6	O	97	al	.
B	5	6	16	M	63	al	.
B	5	13	6	M	60	al	.
B	5	6	16	M	63	al	.
B	5	13	6	M	60	al	.
B	5	14	12	M	74	al	.
B	5	5	6	M	67	al	.
B	5	7	49	M	98	al	.
B	5	6	16	M	70	al	.
B	5	14	12	M	74	al	.
B	5	7	49	M	98	al	.
B	5	6	16	M	70	al	.
B	5	13	6	M	74	al	.
B	5	6	16	M	70	al	.
B	5	5	6	M	69	al	.

B	5	7	49	M	98	al	.
B	5	13	6	M	74	al	.
B	5	14	12	M	74	al	.
B	5	5	6	M	67	al	.
B	5	7	49	M	98	al	.
B	5	6	16	M	71	al	.
B	5	13	6	M	74	al	.
B	5	14	12	M	74	al	.
B	5	5	6	M	67	al	.
B	5	6	16	M	74	og	20.0
B	5	6	16	M	68	og	26.0
B	5	13	6	.	.	sc	20.5
B	5	6	16	M	70	og	22.5
B	5	7	49	M	98	al	.
B	5	5	6	M	67	al	.
B	5	14	12	M	74	al	.
B	5	5	6	M	67	al	.
B	5	14	12	M	74	al	.
B	5	5	6	M	67	al	.
B	5	7	49	M	98	al	.
B	5	14	12	M	74	al	.
B	5	5	6	M	67	al	.
B	5	7	49	M	98	al	.
B	5	13	6	O	94	al	.
B	5	5	6	M	67	al	.
B	5	14	12	M	74	al	.
H	2	13	1	O	96	al	.
H	2	12	5	O	72	al	.
H	2	13	1	O	96	al	.
H	2	5	7	O	97	al	.
H	2	6	8	O	97	al	.
H	2	14	4	O	87	al	.
H	2	12	5	O	89	al	.
H	2	5	7	O	97	al	.
H	2	13	1	O	96	al	.
H	2	12	5	O	89	al	.
H	2	5	7	O	97	al	.
H	2	15	6	O	80	al	.
H	2	14	4	O	87	al	.
H	2	13	1	O	96	al	.
H	2	5	7	O	97	al	.
H	2	6	8	O	92	al	.
H	2	12	5	O	98	al	.
H	2	5	7	O	95	al	.
H	2	6	8	O	92	al	.
H	2	13	1	O	100	al	.

H	2	12	5	O	98	al	.
H	2	5	7	O	95	al	.
H	2	5	7	O	95	al	.
H	2	6	8	O	97	al	.
H	2	5	7	O	95	al	.
H	2	6	8	O	97	al	.
H	2	15	6	O	92	fg	.
H	2	14	4	O	82	cu	20.5
H	2	5	7	O	85	at	.
H	2	15	6	O	88	hg	.
H	2	12	5	O	72	at	.
H	2	15	6	O	88	cu	20.5
H	2	15	6	O	94	at	.
H	2	6	8	O	97	at	.
H	2	12	5	O	89	hg	.
H	2	15	6	O	80	mo	26.0
H	2	5	7	O	97	at	.
H	2	15	6	O	91	fg	.
H	2	15	6	O	97	hg	.
H	2	6	8	O	92	at	.
H	2	15	6	O	90	hg	.
H	2	15	6	O	81	hg	.
H	2	14	4	O	99	hg	.
H	2	13	1	O	100	hg	.
H	2	12	5	O	92	fg	.
H	2	13	1	O	96	al	.
H	2	14	4	O	87	al	.
H	2	13	1	O	96	al	.
H	2	6	8	O	92	al	.
H	2	12	5	O	98	al	.
H	2	13	1	O	100	al	.
H	2	6	8	O	97	al	.
H	2	14	4	O	90	at	.
H	2	6	8	O	97	at	.
H	2	14	4	O	100	hg	.
H	2	14	4	O	96	hg	.
H	2	14	4	O	81	hg	.
H	2	12	5	O	98	at	.
H	2	8	2	O	97	al	.
H	2	9	39	O	110	al	.
H	2	10	25	O	92	al	.
H	2	11	2	O	96	al	.
H	2	7	56	M	72	al	.
H	2	8	2	O	88	al	.
H	2	9	39	O	110	al	.
H	2	11	2	O	96	al	.

H	2	7	56	M	72	al	.
H	2	8	2	O	88	al	.
H	2	8	2	O	98	al	.
H	2	11	2	O	87	al	.
H	2	7	56	O	98	al	.
H	2	9	39	O	86	al	.
H	2	7	56	O	98	al	.
H	2	8	2	O	83	al	.
H	2	9	39	O	86	al	.
H	2	8	2	O	83	al	.
H	2	9	39	O	86	al	.
H	2	10	25	O	102	al	.
H	2	11	2	O	97	al	.
H	2	9	39	O	86	al	.
H	2	7	56	O	101	al	.
H	2	8	2	O	83	al	.
H	2	9	39	O	86	al	.
H	2	10	25	O	96	al	.
H	2	11	2	M	72	al	.
H	2	7	56	O	101	al	.
H	2	8	2	O	83	al	.
H	2	9	39	O	86	al	.
H	2	10	25	O	96	al	.
H	2	7	56	O	89	og	21.0
H	2	10	25	O	92	sc	16.0
H	2	8	2	O	98	at	.
H	2	10	25	M	68	cu	16.5
H	2	11	2	O	100	hg	.
H	2	7	56	O	98	og	25.0
H	2	11	2	M	72	fg	.
H	2	11	2	O	87	al	.
H	2	8	2	O	83	al	.
H	2	10	25	O	91	hg	.
H	2	9	39	O	110	al	.
H	2	7	56	O	98	al	.
H	3	15	6	O	82	al	.
H	3	14	4	O	92	al	.
H	3	12	5	O	94	al	.
H	3	12	5	O	94	al	.
H	3	5	7	O	82	al	.
H	3	14	4	O	98	al	.
H	3	12	5	O	94	al	.
H	3	14	4	O	94	al	.
H	3	5	7	O	90	al	.
H	3	14	4	O	94	al	.
H	3	13	1	O	84	al	.

H	3	5	7	O	90	al	.
H	3	13	1	O	84	al	.
H	3	12	5	O	89	al	.
H	3	5	7	O	90	al	.
H	3	12	5	O	89	al	.
H	3	5	7	O	90	al	.
H	3	14	4	O	91	hg	.
H	3	13	1	O	92	hg	.
H	3	12	5	O	91	hg	.
H	3	5	7	M	62	fg	.
H	3	15	6	O	82	fg	.
H	3	14	4	O	95	hg	.
H	3	13	1	M	69	hg	.
H	3	12	5	O	92	hg	.
H	3	5	7	O	90	hg	.
H	3	15	6	O	97	hg	.
H	3	14	4	O	92	hg	.
H	3	13	1	O	97	hg	.
H	3	12	5	O	94	hg	.
H	3	5	7	O	98	hg	.
H	3	15	6	O	94	mo	26.0
H	3	13	1	M	66	fg	.
H	3	5	7	M	61	cu	15.0
H	3	15	6	.	.	fg	.
H	3	14	4	O	92	at	.
H	3	15	6	O	97	hg	.
H	3	13	1	O	88	hg	.
H	3	5	7	O	82	at	.
H	3	15	6	O	99	hg	.
H	3	13	1	O	93	hg	.
H	3	12	5	O	84	at	.
H	3	15	6	O	93	hg	.
H	3	15	6	O	92	hg	.
H	3	14	4	O	94	fg	.
H	3	15	6	O	94	hg	.
H	3	14	4	O	93	hg	.
H	3	13	1	.	.	hg	.
H	3	13	1	O	84	hg	.
H	3	6	8	M	60	al	.
H	3	9	39	O	89	al	.
H	3	8	2	O	90	al	.
H	3	7	56	O	90	al	.
H	3	9	39	O	89	al	.
H	3	8	2	O	90	al	.
H	3	11	2	O	97	al	.
H	3	8	2	O	90	al	.

H	3	11	2	O	94	og	20.0
H	3	10	25	M	67	og	16.0
H	3	11	2	M	56	sc	13.0
H	3	6	8	M	60	fg	.
H	3	10	25	M	58	cu	14.0
H	3	7	56	M	58	og	24.0
H	3	6	8	M	66	hg	.
H	3	10	25	M	68	sc	15.5
H	3	9	39	O	89	og	50.0
H	3	7	56	O	98	og	22.0
H	4	7	56	M	64	og	16.5
H	4	10	25	M	61	al	.
H	4	11	2	M	75	al	.
H	4	11	2	M	75	al	.
H	4	7	56	M	60	al	.
H	4	11	2	M	72	al	.
H	4	6	8	M	71	al	.
H	4	11	2	M	72	al	.
H	4	7	56	M	55	mo	23.0
H	4	6	8	M	74	hg	.
H	4	7	56	M	66	og	22.0
H	4	8	2	M	58	hg	.
H	4	6	8	M	60	hg	.
H	4	10	25	M	70	hg	.
H	4	6	8	M	73	hg	.
H	4	10	25	M	71	hg	.
H	4	9	39	M	70	hg	.
H	4	8	2	M	80	al	.
H	4	8	2	M	74	hg	.
H	4	9	39	M	58	hg	.
H	4	9	39	M	64	al	.
H	4	8	2	M	80	al	.
H	4	8	2	M	66	al	.
H	4	11	2	M	68	al	.
H	4	6	8	M	75	al	.
H	4	8	2	M	66	al	.
H	4	10	25	M	78	al	.
H	4	6	8	M	75	al	.
H	4	11	2	M	65	al	.
H	4	7	56	M	67	hg	.
H	4	9	39	M	58	og	17.0
H	4	6	8	M	62	hg	.
H	4	7	56	M	66	og	31.0
H	4	9	39	M	60	hg	.
H	4	10	25	M	64	hg	.
H	4	7	56	M	57	cu	16.0

H	4	9	39	M	58	hg	.
H	4	8	2	M	66	al	.
H	4	11	2	M	65	al	.
H	4	10	25	M	57	hg	.
H	4	14	4	M	57	al	.
H	4	15	6	M	87	al	.
H	4	5	7	M	80	al	.
H	4	13	1	M	75	al	.
H	4	5	7	M	80	al	.
H	4	15	6	M	67	al	.
H	4	12	5	M	74	al	.
H	4	15	6	M	67	al	.
H	4	14	4	M	55	al	.
H	4	13	1	M	82	al	.
H	4	5	7	M	67	al	.
H	4	15	6	M	67	al	.
H	4	14	4	M	55	al	.
H	4	13	1	M	82	al	.
H	4	5	7	M	67	al	.
H	4	14	4	M	55	al	.
H	4	12	5	M	64	al	.
H	4	14	4	M	55	al	.
H	4	14	4	M	55	al	.
H	4	12	5	M	71	al	.
H	4	13	1	M	58	al	.
H	4	12	5	M	71	al	.
H	4	5	7	M	63	al	.
H	4	15	6	M	82	hg	.
H	4	13	1	M	62	hg	.
H	4	12	5	M	55	hg	.
H	4	5	7	M	57	hg	.
H	4	14	4	M	57	hg	.
H	4	13	1	M	56	fg	.
H	4	12	5	M	82	hg	.
H	4	15	6	M	87	hg	.
H	4	14	4	M	78	og	35.0
H	4	12	5	M	64	og	16.0
H	4	14	4	M	70	hg	.
H	4	13	1	M	77	mo	25.0
H	4	5	7	M	80	hg	.
H	4	12	5	M	74	hg	.
H	4	12	5	M	67	hg	.
H	4	15	6	M	67	hg	.
H	4	13	1	M	82	hg	.
H	4	5	7	M	67	hg	.
H	4	15	6	M	57	hg	.

H	4	13	1	M	59	hg	.
H	4	5	7	M	49	hg	.
H	4	15	6	M	68	mo	20.5
H	4	13	1	M	55	hg	.
H	4	5	7	M	68	at	.
H	4	15	6	M	55	mo	23.0
H	4	14	4	M	55	hg	.
H	4	9	39	M	62	al	.
H	4	11	2	M	57	al	.
H	4	7	56	M	62	al	.
H	4	8	2	M	53	al	.
H	4	11	2	M	73	al	.
H	4	11	2	M	56	al	.
H	4	8	2	M	63	al	.
H	4	9	39	M	59	al	.
H	4	11	2	M	56	al	.
H	4	9	39	M	59	al	.
H	4	11	2	M	56	al	.
H	4	7	56	M	73	al	.
H	4	11	2	M	52	al	.
H	4	7	56	M	73	al	.
H	4	11	2	M	52	al	.
H	4	7	56	M	52	hg	.
H	4	8	2	M	66	hg	.
H	4	10	25	M	77	fg	.
H	4	8	2	M	71	hg	.
H	4	9	39	M	62	fg	.
H	4	10	25	M	64	fg	.
H	4	11	2	M	57	og	24.5
H	4	7	56	M	62	sc	20.0
H	4	9	39	M	56	og	20.5
H	4	8	2	M	53	mo	16.0
H	4	9	39	M	68	fg	.
H	4	10	25	M	89	hg	.
H	4	11	2	M	73	og	16.5
H	4	8	2	M	73	og	16.0
H	4	9	39	M	58	hg	.
H	4	7	56	M	63	og	22.0
H	4	10	25	M	55	fg	.
H	4	8	2	M	63	sc	14.5
H	4	10	25	M	77	og	22.0
H	4	7	56	M	.	og	23.0
H	4	8	2	M	77	hg	.
H	4	10	25	M	61	og	23.0
H	4	11	2	M	63	fg	.
H	4	8	2	M	82	hg	.

H	4	9	39	M	71	hg	.
H	4	10	25	M	75	og	30.0
H	4	8	2	M	52	fg	.
H	4	9	39	M	77	fg	.
H	4	10	25	M	55	fg	.
H	4	7	56	M	73	hg	.
H	4	10	25	M	57	fg	.
H	4	7	56	M	77	sc	18.0
H	4	10	25	M	55	al	.
M	1	6	3	O	84	al	.
M	1	3	30	O	81	al	.
M	1	2	10	M	56	fg	.
M	1	7	9	M	55	fg	.
M	1	6	3	O	73	at	.
M	1	4	15	O	81	cu	16.0
M	1	4	15	M	59	fg	.
M	1	7	9	O	87	at	.
M	1	4	15	O	81	fg	.
M	1	7	9	O	78	cu	14.0
M	1	14	48	M	59	cu	19.0
M	1	14	48	O	87	fg	.
M	1	10	20	M	57	cu	19.0
M	1	12	1	M	64	fg	.
M	1	9	1	O	79	sc	26.0
M	1	10	20	O	80	hg	.
M	1	12	1	M	65	cu	17.0
M	1	9	1	O	89	fg	.
M	1	13	3	O	79	cu	19.5
M	1	12	1	O	81	cu	18.0
M	1	9	1	O	78	fg	.
M	1	14	48	M	64	fg	.
M	1	13	3	O	92	fg	.
M	1	10	20	O	79	cu	17.0
M	1	13	3	O	80	hg	.
M	1	14	48	O	78	hg	.
M	1	10	20	M	54	fg	.
M	1	10	20	O	94	hg	.
M	1	3	30	O	90	at	.
M	1	4	15	O	87	cu	18.0
M	1	3	30	O	77	hg	.
M	1	11	1	O	88	hg	.
M	1	3	30	O	81	hg	.
M	1	5	4	O	87	hg	.
M	1	5	4	O	94	at	.
M	1	4	15	O	88	cu	18.0
M	1	3	30	O	94	at	.

M	1	8	6	O	81	hg	.
M	1	5	4	O	89	hg	.
M	1	5	4	O	94	hg	.
M	1	4	15	O	83	hg	.
M	1	11	1	O	81	mo	20.0
M	1	5	4	O	89	hg	.
M	1	5	4	O	89	fg	.
M	1	4	15	O	90	fg	.
M	1	8	6	O	86	fg	.
M	1	11	1	O	85	cu	18.5
M	1	8	6	O	88	hg	.
M	1	5	4	O	83	cu	21.0
M	1	8	6	O	84	cu	17.0
M	2	3	30	O	77	al	.
M	2	3	30	O	77	al	.
M	2	2	10	O	84	al	.
M	2	2	10	M	68	al	.
M	2	6	3	O	103	al	.
M	2	2	10	O	97	al	.
M	2	6	3	O	103	al	.
M	2	3	30	O	88	al	.
M	2	2	10	O	97	al	.
M	2	6	3	O	103	al	.
M	2	7	9	O	93	hg	.
M	2	2	10	O	100	og	29.0
M	2	6	3	O	90	at	.
M	2	7	9	O	87	og	50.0
M	2	2	10	O	92	og	40.0
M	2	6	3	O	90	og	25.0
M	2	6	3	O	90	at	.
M	2	7	9	O	83	hg	.
M	2	6	3	O	84	hg	.
M	2	7	9	O	98	hg	.
M	2	3	30	O	97	at	.
M	2	3	30	M	67	og	23.0
M	2	6	3	O	103	mo	35.0
M	2	7	9	O	95	at	.
M	2	3	30	O	90	fg	.
M	2	7	9	O	96	hg	.
M	2	6	3	O	89	al	.
M	3	2	10	M	55	al	.
M	3	2	10	M	55	al	.
M	3	4	15	M	68	fg	.
M	3	8	6	M	58	fg	.
M	3	5	4	M	64	og	19.0
M	3	5	4	M	55	hg	.

M	3	4	15	M	72	og	24.0
M	4	9	1	O	82	al	.
M	4	12	1	O	85	al	.
M	4	10	20	O	92	al	.
M	4	13	3	O	94	al	.
M	4	13	3	O	93	al	.
M	4	14	48	O	93	og	25.0
M	4	10	20	O	89	at	.
M	4	13	3	O	87	hg	.
M	4	12	1	O	83	og	27.0
M	4	14	48	O	102	at	.
M	4	10	20	O	98	og	22.0
M	4	13	3	O	90	og	33.0
M	4	14	48	O	88	at	.
M	4	10	20	O	98	fg	.
M	4	13	3	O	83	sc	16.5
M	4	9	1	O	96	at	.
M	4	14	48	O	95	fg	.
M	4	9	1	O	96	hg	.
M	4	14	48	O	88	fg	.
M	4	10	20	O	89	hg	.
M	4	13	3	O	94	og	21.0
M	4	10	20	M	60	fg	.
M	4	13	3	O	98	hg	.
M	4	12	1	O	98	fg	.
M	4	9	1	M	75	hg	.
M	4	14	48	O	93	hg	.
M	4	10	20	O	93	hg	.
M	4	13	3	O	94	hg	.
M	4	12	1	O	94	at	.
M	4	9	1	O	101	at	.
M	4	14	48	O	95	fg	.
M	4	10	20	O	92	at	.
M	4	9	1	O	97	sc	29.0
M	4	10	20	O	92	hg	.
M	4	13	3	O	96	fg	.
M	4	12	1	O	98	fg	.
M	4	10	20	.	.	fg	.
M	4	12	1	O	93	hg	.
M	4	9	1	O	100	hg	.
M	4	14	48	O	97	fg	.
M	4	9	1	O	82	al	.
M	4	12	1	O	85	al	.
M	4	13	3	O	92	al	.
M	4	14	48	M	61	hg	.
M	4	12	1	O	92	hg	.

M	4	4	15	O	93	al	.
M	4	5	4	O	93	al	.
M	4	8	6	O	86	al	.
M	4	2	10	O	99	al	.
M	4	11	1	M	67	al	.
M	4	4	15	O	93	al	.
M	4	8	6	O	86	al	.
M	4	4	15	O	92	al	.
M	4	8	6	O	86	al	.
M	4	2	10	M	70	al	.
M	4	11	1	O	102	hg	.
M	4	2	10	O	91	og	19.5
M	4	11	1	M	67	hg	.
M	4	5	4	O	93	hg	.
M	4	5	4	O	93	sc	19.5
M	4	5	4	M	67	al	.
M	4	8	6	O	97	al	.
M	4	11	1	O	87	fg	.
M	4	4	15	O	88	og	30.5
M	4	2	10	M	57	al	.
M	4	8	6	M	69	al	.
M	4	2	10	M	57	al	.
M	4	11	1	M	62	al	.
M	4	2	10	M	62	al	.
M	4	11	1	M	63	og	32.0
M	4	4	15	M	53	hg	.
M	4	8	6	M	69	og	30.0
M	4	11	1	M	63	hg	.
M	4	4	15	M	58	og	27.0
M	4	8	6	M	83	og	26.5
M	4	11	1	M	68	hg	.
M	4	4	15	M	67	hg	.
M	4	5	4	M	61	og	22.5
M	4	4	15	M	68	hg	.
M	4	5	4	M	61	hg	.
M	4	4	15	M	67	hg	.
M	4	5	4	M	69	hg	.
M	4	8	6	M	69	hg	.
M	4	5	4	M	61	sc	15.5
M	4	2	10	M	62	sc	23.5
M	4	2	10	M	57	al	.
M	4	8	6	M	69	al	.
M	4	2	10	M	57	al	.
M	4	1	6	M	62	al	.
M	4	1	6	M	62	al	.
M	4	6	3	M	52	al	.

M	4	1	6	M	62	al	.
M	4	6	3	M	52	al	.
M	4	3	30	M	78	al	.
M	4	3	30	M	78	al	.
M	4	1	6	M	62	at	.
M	4	7	9	M	61	hg	.
M	4	7	9	M	62	sc	18.5
M	4	3	30	M	72	hg	.
M	4	7	9	M	61	hg	.
M	4	3	30	M	65	at	.
M	4	7	9	M	69	hg	.
M	4	1	6	M	62	hg	.
M	4	6	3	M	56	og	19.0
M	4	1	6	M	54	hg	.
M	4	3	30	M	70	og	15.0
M	4	6	3	M	64	hg	.
M	4	7	9	M	75	sc	20.0
M	4	1	6	M	62	og	30.0
M	4	3	30	M	62	hg	.
M	4	3	30	M	54	hg	.
M	4	7	9	M	64	hg	.
M	4	1	6	M	64	og	22.5
M	4	1	6	M	60	hg	.
M	4	6	3	M	52	al	.
M	4	7	9	M	56	hg	.
M	4	1	6	M	59	sc	22.0
M	4	3	30	M	64	fg	.
M	4	7	9	M	57	hg	.
M	4	3	30	M	67	hg	.
M	4	6	3	M	60	al	.
M	4	7	9	M	58	al	.
M	4	7	9	M	58	al	.
M	4	6	3	M	51	al	.
M	5	6	3	M	64	al	.
M	5	7	9	M	70	al	.
M	5	2	10	M	61	al	.
M	5	2	10	M	61	al	.
M	5	6	3	M	63	al	.
M	5	6	3	M	71	al	.
M	5	2	10	M	56	al	.
M	5	3	30	M	67	al	.
M	5	2	10	M	55	al	.
M	5	3	30	M	58	al	.
M	5	1	6	M	55	hg	.
M	5	3	30	M	70	hg	.
M	5	1	6	M	57	hg	.

M	5	3	30	M	63	og	20.0
M	5	6	3	M	64	hg	.
M	5	7	9	M	70	fg	.
M	5	7	9	M	82	hg	.
M	5	1	6	M	62	sc	18.0
M	5	7	9	M	72	hg	.
M	5	1	6	M	77	hg	.
M	5	3	30	M	62	hg	.
M	5	7	9	M	67	fg	.
M	5	1	6	M	56	hg	.
M	5	6	3	M	71	hg	.
M	5	1	6	M	70	hg	.
M	5	3	30	M	67	hg	.
M	5	2	10	M	67	hg	.
M	5	1	6	M	61	hg	.
M	5	3	30	M	62	hg	.
M	5	6	3	M	64	hg	.
M	5	7	9	M	71	hg	.
M	5	1	6	M	87	hg	.
M	5	6	3	M	62	hg	.
M	5	7	9	M	60	hg	.
M	5	2	10	M	55	og	11.2
M	5	1	6	M	89	og	19.0
M	5	3	30	M	58	hg	.
M	5	6	3	M	63	fg	.
M	5	7	9	M	74	hg	.
M	5	2	10	M	68	sc	15.5
M	5	2	10	M	61	al	.
M	5	2	10	M	61	fg	.
M	5	7	9	M	58	og	25.0
M	5	6	3	M	65	sc	20.5
M	5	7	9	M	67	hg	.
M	5	8	6	M	65	al	.
M	5	8	6	M	57	al	.
M	5	5	4	O	87	al	.
M	5	9	1	M	58	al	.
M	5	9	1	M	58	al	.
M	5	11	1	M	66	al	.
M	5	9	1	M	65	al	.
M	5	8	6	O	91	al	.
M	5	9	1	M	65	al	.
M	5	5	4	M	60	hg	.
M	5	4	15	M	65	hg	.
M	5	11	1	M	63	og	19.5
M	5	8	6	M	65	fg	.
M	5	5	4	M	74	og	26.5

M	5	11	1	O	96	hg	.
M	5	9	1	O	94	hg	.
M	5	4	15	O	78	hg	.
M	5	11	1	M	78	og	27.0
M	5	8	6	M	57	fg	.
M	5	5	4	O	87	hg	.
M	5	4	15	M	82	hg	.
M	5	11	1	O	90	hg	.
M	5	8	6	M	62	hg	.
M	5	5	4	M	62	fg	.
M	5	4	15	M	58	hg	.
M	5	11	1	M	75	fg	.
M	5	9	1	M	58	og	26.5
M	5	5	4	M	61	hg	.
M	5	4	15	M	78	og	31.5
M	5	5	4	M	67	hg	.
M	5	4	15	O	92	fg	.
M	5	11	1	M	66	og	28.5
M	5	8	6	O	91	al	.
M	5	9	1	O	82	al	.
M	5	8	6	M	66	hg	.
M	5	5	4	M	54	hg	.
M	5	4	15	O	87	hg	.
M	5	11	1	M	77	fg	.
M	5	8	6	O	88	sc	17.5
M	5	4	15	O	85	hg	.
M	5	11	1	M	79	sc	19.5
M	5	9	1	O	82	hg	.
M	5	8	6	O	80	hg	.
M	5	5	4	M	62	hg	.
M	5	4	15	M	65	og	22.0
M	5	11	1	M	67	hg	.
M	5	9	1	O	77	hg	.
M	5	5	4	M	58	sc	19.0
M	5	10	20	M	70	al	.
M	5	12	1	M	78	al	.
M	5	12	1	M	78	al	.
M	5	12	1	M	78	al	.
M	5	13	3	O	90	fg	.
M	5	12	1	O	92	hg	.
M	5	10	20	M	81	hg	.
M	5	14	48	M	72	sc	24.5
M	5	13	3	M	60	hg	.
M	5	12	1	M	57	hg	.
M	5	10	20	O	85	sc	20.5
M	5	14	48	M	58	og	33.5

M	5	13	3	M	73	hg	.
M	5	12	1	M	81	fg	.
M	5	10	20	M	61	hg	.
M	5	13	3	M	62	og	30.0
M	5	12	1	M	76	hg	.
M	5	14	48	M	58	fg	.
M	5	13	3	M	70	hg	.
M	5	12	1	M	53	hg	.
M	5	10	20	M	70	hg	.
M	5	14	48	M	80	hg	.
M	5	13	3	M	76	og	30.0
M	5	12	1	M	62	hg	.
M	5	10	20	M	74	fg	.
M	5	14	48	M	60	hg	.
M	5	13	3	M	70	hg	.
M	5	12	1	M	69	og	21.5
M	5	10	20	M	66	og	29.0
M	5	13	3	M	59	hg	.
M	5	10	20	M	76	at	.
M	5	13	3	M	72	mo	25.0
M	5	10	20	M	71	hg	.
M	5	13	3	M	63	hg	.
M	5	14	48	M	69	hg	.
T	9	14	15	m	75	al	.
T	9	15	2	o	95	fg	.
T	9	13	.	m	80	al	.
T	9	16	3	o	91	og	30.5
T	9	17	6	o	84	hg	.
T	9	14	15	m	75	al	.
T	9	15	2	o	93	fg	.
T	9	13	.	m	80	al	.
T	9	16	3	o	88	hg	.
T	9	17	6	o	92	al	.
T	9	12	80	m	75	al	.
T	9	19	70	o	96	hg	.
T	9	8	6	m	80	al	.
T	9	20	24	o	92	at	.
T	9	21	4	o	92	hg	.
T	9	12	80	m	75	cu	19.0
T	9	19	70	o	92	al	.
T	9	8	6	m	80	fg	.
T	9	20	24	m	66	hg	.
T	9	21	4	m	87	fg	.
T	9	11	1	o	92	al	.
T	9	10	7.5	o	92	al	.
T	9	22	20	o	92	mo	25.0

T	9	23	64	m	70	al	.
T	9	24	.	o	95	al	.
T	9	11	1	o	92	al	.
T	9	10	7.5	o	92	al	.
T	9	22	20	m	66	fg	.
T	9	24	64	o	95	al	.
T	9	32	40	o	92	og	24.0
T	9	3	2	m	58	sc	20.0
T	9	23	64	m	69	fg	.
T	9	29	26	o	95	al	.
T	9	25	6	o	92	hg	.
T	9	32	40	m	61	cu	15.0
T	9	30	48	m	60	al	.
T	9	29	26	o	95	al	.
T	9	1	12	m	58	og	26.0
T	9	2	22	m	80	og	19.0
T	9	27	35	o	95	og	25.0
T	9	26	20	m	95	al	.
T	9	1	12	m	55	fg	.
T	9	2	22	m	70	fg	.
T	9	27	35	m	78	fg	.
T	9	34	6	m	58	cu	11.0
T	9	26	20	m	95	og	23.5
T	9	33	.	o	92	og	24.0
T	9	28	16	m	62	fg	.
T	9	6	1	o	97	at	.
T	9	34	6	o	87	sc	27.0
T	9	28	16	o	98	hg	.
T	9	6	1	o	95	fg	.
T	9	33	.	o	94	fg	.
T	9	1	12	o	100	hg	.
T	9	27	35	o	77	hg	.
T	9	2	22	o	81	og	24.5
T	9	26	20	o	81	hg	.
T	9	34	6	o	100	hg	.
T	9	33	.	o	95	hg	.
T	9	28	16	o	95	og	23.0
T	9	6	1	o	92	hg	.
T	9	29	26	o	92	hg	.
T	9	3	2	o	100	al	.
T	9	30	48	o	102	hg	.
T	9	32	40	o	95	al	.
T	9	25	6	o	94	hg	.
T	9	24	.	o	93	al	.
T	9	23	64	o	100	fg	.
T	9	19	70	o	93	al	.

T	9	22	20	o	105	hg	.
T	9	21	4	o	100	hg	.
T	9	20	24	o	90	hg	.
T	9	35	4	o	93	al	.
T	9	8	6	o	100	hg	.
T	9	10	7.5	m	94	al	.
T	9	11	1	o	95	al	.
T	9	20	24	o	96	hg	.
T	9	35	4	o	93	cu	26.0
T	9	12	80	o	88	al	.
T	9	17	6	m	94	al	.
T	9	15	2	o	100	hg	.
T	9	35	4	o	98	fg	.
T	9	14	15	o	88	hg	.
T	9	11	1	o	100	al	.
T	9	13	.	o	92	at	.
T	9	16	3	o	100	fg	.
T	9	1	12	m	91	hg	.
T	9	27	35	o	99	hg	.
T	9	34	6	o	96	fg	.
T	9	28	16	o	99	al	.
T	9	29	26	o	97	og	17.5
T	9	3	2	o	98	hg	.
T	9	23	64	o	91	fg	.
T	9	25	6	m	76	al	.
T	9	24	.	o	102	al	.
T	9	22	20	o	95	at	.
T	9	21	4	o	98	hg	.
T	9	8	6	m	76	al	.
T	9	35	4	o	102	al	.
T	9	20	24	o	84	hg	.
T	9	10	7.5	o	94	hg	.
T	9	11	1	o	97	al	.
T	9	12	80	o	102	al	.
T	9	17	6	o	97	hg	.
T	9	16	3	o	96	og	21.5
T	9	14	15	o	97	al	.
T	9	13	.	o	102	at	.
T	9	17	6	o	93	al	.
T	9	16	3	m	88	hg	.
T	9	15	2	o	99	hg	.
T	9	14	15	o	97	al	.
T	9	13	.	o	88	hg	.
T	9	11	1	o	93	al	.
T	9	10	7.5	o	94	al	.
T	9	12	80	o	96	hg	.

T	9	35	4	o	97	at	.
T	9	8	6	m	84	hg	.
T	9	19	70	o	93	al	.
T	9	20	24	o	94	al	.
T	9	21	4	o	97	hg	.
T	9	22	20	o	101	hg	.
T	9	23	64	m	84	hg	.
T	9	3	2	o	93	fg	.
T	9	25	6	o	94	hg	.
T	9	32	40	o	88	fg	.
T	9	29	26	o	95	at	.
T	9	30	48	o	78	hg	.
T	9	28	16	o	103	fg	.
T	9	33	.	o	95	fg	.
T	9	34	6	o	103	al	.
T	9	26	20	o	102	hg	.
T	9	2	22	o	100	hg	.
T	9	27	35	o	98	hg	.
T	9	1	12	o	97	fg	.
T	9	1	12	o	96	hg	.
T	9	2	22	o	90	hg	.
T	9	27	35	m	91	og	24.5
T	9	26	20	o	99	hg	.
T	9	34	6	o	99	fg	.
T	9	33	.	m	76	og	24.0
T	9	28	16	o	97	hg	.
T	9	6	1	m	88	cu	18.0
T	9	29	26	o	95	al	.
T	9	30	48	m	84	sc	19.5
T	9	32	40	o	103	hg	.
T	9	3	2	o	97	al	.
T	9	25	6	m	84	al	.
T	9	23	64	o	95	al	.
T	9	22	20	o	97	hg	.
T	9	21	4	o	93	hg	.
T	9	20	24	o	97	al	.
T	9	19	70	m	84	al	.
T	9	8	6	o	95	hg	.
T	9	35	4	m	97	at	.
T	9	10	7.5	m	90	al	.
T	9	11	1	o	97	al	.
T	9	12	80	m	84	al	.
T	9	17	6	o	91	al	.
T	9	16	3	o	107	al	.
T	9	15	2	m	90	hg	.
T	9	14	15	o	97	hg	.

T	9	13	.	m	84	fg	.
T	9	26	20	o	107	hg	.
T	9	14	15	o	96	hg	.
T	9	15	2	o	102	hg	.
T	9	13	.	o	92	at	.
T	9	16	3	o	103	hg	.
T	9	17	6	o	94	hg	.
T	9	12	80	o	91	al	.
T	9	11	1	o	102	hg	.
T	9	10	7.5	o	91	hg	.
T	9	35	4	m	88	fg	.
T	9	19	70	o	91	hg	.
T	9	20	24	o	100	al	.
T	9	21	4	o	96	hg	.
T	9	22	20	o	104	hg	.
T	9	23	64	o	102	hg	.
T	9	25	6	o	100	fg	.
T	9	32	40	o	96	fg	.
T	9	3	2	o	98	fg	.
T	9	29	26	o	92	al	.
T	9	8	6	o	100	al	.
T	9	30	48	o	96	hg	.
T	9	6	1	o	97	hg	.
T	9	28	16	o	92	al	.
T	9	33	.	o	100	fg	.
T	9	34	6	o	104	al	.
T	9	26	20	o	89	hg	.
T	9	2	22	o	92	hg	.
T	9	27	35	o	97	hg	.
T	9	1	12	o	104	hg	.
T	9	1	12	o	111	hg	.
T	9	27	35	o	108	hg	.
T	9	2	22	o	101	al	.
T	9	26	20	m	70	hg	.
T	9	34	6	o	92	hg	.
T	9	33	.	o	100	hg	.
T	9	28	16	m	67	og	20.0
T	9	30	48	o	101	at	.
T	9	29	26	o	85	al	.
T	9	6	1	o	97	hg	.
T	9	32	40	o	68	hg	.
T	9	3	2	o	92	al	.
T	9	25	6	o	98	og	27.0
T	9	23	64	o	85	hg	.
T	9	22	20	m	72	al	.
T	9	21	4	o	104	al	.

T	9	20	24	o	92	al	.
T	9	8	6	o	84	al	.
T	9	35	4	o	87	al	.
T	9	19	70	m	72	al	.
T	9	10	7.5	o	92	al	.
T	9	11	1	m	81	al	.
T	9	12	80	o	94	al	.
T	9	17	6	o	97	al	.
T	9	16	3	m	72	at	.
T	9	13	.	o	97	at	.
T	9	15	2	m	81	sc	21.5
T	9	14	15	o	97	al	.

Appendix E: Raw data from the Edge Effects Study (Chapter 3)

s	d	sub	tsp	lsl	out	bsl
B	1	m2	o	71	fg	
B	1	m1	o	68	fg	
B	1	m1	o	63	fg	
B	1	m2	o	68	fg	
B	1	m1	o	64	og	13.00
B	1	m1	o	68	fg	
B	1	m2	o	69	cu	14.00
B	1	m1	o	72	fg	
B	1	m1	o	62	fg	
B	1	m2	o	68	fg	
B	1	m1	o	57	fg	
B	1	m1	o	62	fg	
B	1	m2	o	66	fg	
B	1	m1	o	62	fg	
B	1	m1	o	71	fg	
B	1	m2	o	62	fg	
B	1	m1	o	67	fg	
B	1	m1	o	67	fg	
B	1	m2	o	69	fg	
B	1	g1	o	60	fg	
B	1	g1	o	58	fg	
B	1	g2	o	71	fg	
B	1	g2	o	68	fg	
B	1	e	o	62	cu	13.00
B	1	e	o	72	fg	
B	1	m2	o	59	fg	
B	1	g1	o	61	fg	
B	1	g1	o	66	fg	
B	1	g2	o	63	fg	
B	1	g2	o	66	fg	
B	1	e	o	64	fg	
B	1	e	o	65	fg	
B	1	m2	o	70	cu	16.00
B	1	g1	o	66	fg	
B	1	g1	o	66	fg	
B	1	g2	o	62	fg	
B	1	g2	o	66	fg	
B	1	e	o	64	fg	
B	1	e	o	61	fg	
B	1	m2	o	61	fg	
B	1	g1	o	66	fg	
B	1	g1	o	76	fg	
B	1	g2	o	66	fg	

Abbreviations	
s	site
d	period
sub	substrate and location
tsp	tethered animal's SL
lsl	tethered animal's spp.
out	outcome
bsl	predator's SL, if caught

site	
B	Buckley's 2000
D	Dockside 2000
sub	
e	edge
g1	Grass 5 m from edge
g2	Grass 10 m from edge
m1	Mud 5 m from edge
m2	Mud 10 m from edge
period	
1	late August
2	early September
3	late September
4	early October
5	late August
6	early September
7	late September
8	early October
tsp	
M	*Gadus morhua*
O	*Gadus ogac*
outcome	
al	alive
at	attacked
cu	cunner
fg	tethered fish gone
ha	hake
hg	hook gone
mo	*Gadus morhua*
og	*Gadus ogac*
sc	sculpin

B	1	g2	o	66	og	17.00
B	1	e	o	72	fg	
B	1	e	o	61	fg	
B	1	m2	o	63	fg	
B	1	g1	o	63	fg	
B	1	g1	o	57	fg	
B	1	g2	o	67	fg	

B	1	g2	o	66	fg	
B	1	e	o	59	fg	
B	1	e	o	66	fg	
B	1	m2	o	64	fg	
B	1	g1	o	66	fg	
B	1	g1	o	62	cu	13.50
B	1	g2	o	68	cu	14.00
B	1	g2	o	64	cu	14.50
D	2	g1	o	68	fg	
D	2	e	o	67	fg	
D	2	m1	m	52	fg	
D	2	m2	o	69	al	
D	2	m2	o	72	al	
D	2	m1	o	70	al	
D	2	e	o	73	al	
D	2	g1	o	71	al	
D	2	g1	o	61	og	17.00
D	2	e	m	51	fg	
D	2	m1	m	52	cu	23.00
D	2	m2	o	69	al	
D	2	m2	o	72	al	
D	2	m1	o	64	sc	22.50
D	2	e	o	73	al	
D	2	g1	o	71	al	
D	2	g1	o	69	al	
D	2	e	o	70	al	
D	2	m1	o	67	cu	12.50
D	2	m2	o	69	al	
D	2	m2	o	72	al	
D	2	m1	m	72	al	
D	2	e	o	73	al	
D	2	g1	o	71	al	
D	2	g1	o	62	og	15.00
D	2	e	o	70	mo	21.00
D	2	m1	o	75	al	
D	2	m2	o	70	al	
D	2	m2	o	67	al	
D	2	m1	o	69	al	

D	5	g1	m	62	at	
D	5	e	.	.	fg	
D	5	m1	m	72	fg	
D	5	m2	m	61	al	
D	5	m2	m	63	al	
D	5	m1	m	54	al	
D	5	e	m	59	al	
D	5	g2	m	64	al	
D	5	g2	m	62	og	17.00
D	5	g1	m	63	al	
D	5	g1	m	62	al	
D	5	g1	m	57	fg	
D	5	g1	m	61	at	
D	5	g2	m	54	al	
D	5	g2	m	59	al	
D	5	g2	m	64	al	
D	5	g2	m	63	og	19.00
D	5	g1	m	62	al	
D	5	m2	m	54	al	
D	5	g1	m	84	al	
D	5	g1	m	59	al	
B	6	g1	m	61	fg	
B	6	e	m	73	cu	17.50
B	6	m2	m	63	fg	
B	6	m2	m	68	cu	14.00
B	6	m1	m	73	og	15.50
B	6	e	m	67	cu	15.50
B	6	g1	m	60	al	
B	6	g1	o	82	fg	
B	6	e	m	74	og	18.00
B	6	m2	o	87	at	
B	6	m2	o	93	al	
B	6	m1	o	95	al	
B	6	e	o	88	al	
B	6	g1	m	60	cu	16.00
B	6	g1	o	83	fg	
B	6	e	o	90	fg	
B	6	m1	o	89	al	

D	2	e	o	72	al	
D	2	g1	m	72	al	
D	2	g1	o	71	fg	
D	2	e	m	69	at	
D	2	m1	o	75	al	
D	2	m2	o	70	al	
D	2	m2	o	67	al	
D	2	m1	o	69	al	
D	2	e	o	72	al	
D	2	g1	m	72	al	
D	2	g1	o	65	fg	
D	2	e	o	72	at	
D	2	m1	o	75	al	
D	2	m2	o	68	al	
D	2	m2	o	67	al	
D	2	m1	o	69	al	
D	2	e	o	72	al	
D	2	g1	m	72	al	
D	2	g2	.	.	al	
D	2	g2	o	73	al	
D	2	g2	o	75	fg	
D	2	g2	o	68	og	18.50
D	2	g2	o	67	al	
D	2	g2	o	69	al	
D	2	g2	o	72	fg	
D	2	g2	o	78	al	
D	2	g2	.	.	al	
D	2	g2	o	74	al	
D	2	g2	o	73	al	
D	2	g2	o	75	al	
B	3	g1	m	61	og	15.00
B	3	e	o	71	fg	
B	3	m1	o	74	al	
B	3	m1	o	72	fg	
B	3	e	o	73	fg	
B	3	g1	o	72	fg	
B	3	g1	m	59	al	
B	3	e	o	79	al	
B	3	m1	o	74	al	
B	3	m1	m	58	fg	
B	3	e	o	80	og	15.00
B	3	g1	o	74	at	
B	3	g1	m	59	fg	
B	3	e	o	79	fg	
B	3	m1	o	74	at	
B	3	m1	o	80	og	16.00

B	6	m2	o	91	al	
B	6	m2	o	93	al	
B	6	m1	o	95	al	
B	6	e	o	88	al	
B	6	g1	o	87	al	
B	6	g1	o	88	cu	17.00
B	6	e	o	94	al	
B	6	m1	o	89	al	
B	6	m2	o	91	at	
B	6	m2	o	93	al	
B	6	m1	o	95	al	
B	6	e	o	88	al	
B	6	g1	o	87	al	
B	6	g1	o	88	al	
B	6	e	o	94	al	
B	6	m1	o	89	al	
B	6	m2	o	92	fg	
B	6	m2	o	93	al	
B	6	m1	o	95	al	
B	6	e	o	88	al	
B	6	g1	o	87	al	
B	6	g1	o	88	hg	
B	6	e	o	78	fg	
B	6	m1	o	89	al	
B	6	m2	o	88	al	
B	6	m2	o	93	al	
B	6	m1	o	86	al	
B	6	e	o	88	al	
B	6	g1	o	87	al	
B	6	g2	o	88	al	
B	6	g2	o	94	al	
B	6	g2	m	74	al	
B	6	g2	o	88	al	
B	6	g2	o	93	al	
B	6	m1	o	88	og	23.00
B	6	g2	m	68	al	
B	6	g2	o	87	al	
B	6	g2	o	88	al	
B	6	g2	o	94	al	
B	6	g2	m	74	al	
B	6	g2	o	88	al	
B	6	g2	o	93	al	
B	6	g2	o	84	al	
B	6	g2	m	68	al	
B	6	g2	o	87	al	
B	6	g2	o	88	al	

B	3	e	o	77	al	
B	3	g1	o	79	fg	
B	3	g1	o	80	at	
B	3	e	o	78	at	
B	3	m1	o	77	al	
B	3	g1	m	57	fg	
B	3	g1	o	78	at	
B	3	e	o	73	fg	
B	3	m1	o	77	al	
B	3	m1	o	77	fg	
B	3	e	o	83	al	
B	3	g1	o	68	fg	
B	3	g1	o	72	al	
B	3	e	o	83	at	
B	3	m1	o	77	og	18.00
B	3	m1	o	77	cu	12.50
B	3	e	o	74	fg	
B	3	g1	o	77	og	19.00
B	3	m1	m	58	fg	
B	3	e	m	54	fg	
B	3	g2	m	58	al	
B	3	g2	o	77	og	15.50
B	3	g2	o	76	al	
B	3	g2	o	81	al	
B	3	g2	o	77	al	
B	3	g2	m	58	og	16.00
B	3	g2	o	76	cu	14.00
B	3	g2	o	81	al	
B	3	m2	o	77	al	
B	3	m2	o	82	al	
B	3	g2	o	68	at	
B	3	g2	o	81	al	
B	3	m2	m	58	fg	
B	3	m2	o	83	al	
B	3	m2	o	82	cu	13.00
B	3	g2	m	62	fg	
B	3	g2	o	81	al	
B	3	m2	o	75	al	
B	3	m2	o	83	al	
B	3	m2	m	57	cu	14.00
B	3	m2	m	60	fg	
B	3	m2	m	59	og	17.50
B	3	m2	o	83	al	
B	3	m2	o	81	fg	
D	4	g1	m	70	al	
D	4	e	o	77	al	

B	6	g2	o	94	at	
B	6	m1	m	74	fg	
D	7	g1	m	72	al	
D	7	e	m	70	al	
D	7	m1	m	72	al	
D	7	m2	m	78	al	
D	7	m2	m	77	al	
D	7	m1	o	82	al	
D	7	e	m	71	al	
D	7	g1	m	72	al	
D	7	m1	m	72	al	
D	7	m2	m	78	al	
D	7	m2	m	77	al	
D	7	m1	o	82	al	
D	7	e	m	71	al	
D	7	g1	o	63	og	17.50
D	7	g1	m	72	al	
D	7	e	m	74	al	
D	7	m1	m	72	al	
D	7	m2	m	78	al	
D	7	m2	m	77	al	
D	7	m1	m	82	al	
D	7	e	m	71	al	
D	7	g1	m	58	al	
D	7	g1	m	72	al	
D	7	e	m	74	al	
D	7	m1	m	72	al	
D	7	m2	m	78	al	
D	7	m2	m	77	al	
D	7	m1	o	82	al	
D	7	e	m	71	at	
D	7	g1	m	58	al	
D	7	g1	m	72	al	
D	7	e	m	74	al	
D	7	m1	m	72	al	
D	7	m2	m	78	al	
D	7	m2	m	77	al	
D	7	m1	o	82	al	
D	7	e	o	86	al	
D	7	g1	m	58	al	
D	7	g1	m	72	al	
D	7	e	m	74	al	
D	7	m1	m	72	al	
D	7	m2	m	78	al	
D	7	m2	m	77	al	
D	7	m1	o	82	al	

D	4	m1	o	64	al	
D	4	m2	o	83	al	
D	4	m2	m	58	al	
D	4	m1	m	58	og	17.50
D	4	e	o	67	fg	
D	4	g1	m	64	al	
D	4	g1	m	70	al	
D	4	e	o	77	at	
D	4	m1	o	64	al	
D	4	m2	o	83	al	
D	4	m2	m	58	al	
D	4	m1	m	72	al	
D	4	e	m	68	at	
D	4	g1	m	64	al	
D	4	g1	m	70	al	
D	4	e	m	64	cu	16.00
D	4	m1	o	64	al	
D	4	m2	o	83	al	
D	4	m2	m	58	al	
D	4	m1	m	72	al	
D	4	e	m	62	al	
D	4	g1	m	64	al	
D	4	g1	m	70	al	
D	4	e	o	77	at	
D	4	m1	o	64	al	
D	4	m2	o	83	al	
D	4	m2	m	58	fg	
D	4	m1	m	72	al	
D	4	e	m	62	at	
D	4	g1	m	64	al	
D	4	g1	m	70	al	
D	4	e	m	68	at	
D	4	m1	o	64	al	
D	4	m2	o	83	al	
D	4	m2	o	78	al	
D	4	m1	m	72	al	
D	4	e	o	73	at	
D	4	g1	m	64	al	
D	4	g1	m	70	al	
D	4	e	m	75	al	
D	4	m1	o	64	al	
D	4	m2	o	83	al	
D	4	m2	o	78	al	
D	4	m1	m	72	al	
D	4	e	m	64	al	
D	4	g1	m	64	al	

D	7	e	o	86	at	
D	7	g1	m	58	al	
D	7	g2	m	72	al	
D	7	g2	m	74	al	
D	7	g2	o	97	sc	13.00
D	7	g2	m	78	al	
D	7	g2	m	77	al	
D	7	g2	o	82	al	
D	7	e	m	78	al	
D	7	g1	m	58	al	
D	7	g2	m	72	al	
D	7	g2	m	74	al	
D	7	g2	m	66	al	
D	7	g2	m	78	al	
D	7	g2	m	77	at	
D	7	g2	o	82	al	
D	7	g2	m	78	al	
D	7	g2	m	58	al	
D	7	g2	m	72	al	
D	7	g2	m	74	al	
D	7	g2	m	66	al	
D	7	g2	m	78	al	
D	7	g2	m	82	al	
D	7	g2	m	77	al	
B	8	g2	m	90	al	
B	8	g1	o	101	al	
B	8	e	m	75	al	
B	8	m1	m	62	al	
B	8	m1	o	90	al	
B	8	e	m	70	og	16.00
B	8	g2	m	90	al	
B	8	g1	o	101	al	
B	8	e	m	75	cu	13.50
B	8	m1	m	62	al	
B	8	m2	o	90	al	
B	8	m1	m	83	sc	21.00
B	8	g2	m	90	al	
B	8	g1	o	101	al	
B	8	m2	o	90	al	
B	8	m2	m	51	al	
B	8	g2	m	90	al	
B	8	g1	o	101	al	
B	8	m1	m	66	og	12.50
B	8	m2	o	90	al	
B	8	m2	m	51	og	19.50
B	8	e	m	84	sc	20.00

D	4	g2	m	70	al	
D	4	g2	m	75	at	
D	4	g2	o	67	og	19.00
D	4	g2	o	83	al	
D	4	g2	o	78	al	
D	4	g2	m	72	sc	16.00
D	4	g2	m	64	al	
D	4	g2	m	64	al	
D	4	g2	m	70	fg	
D	4	g2	o	78	og	17.50
D	4	g2	m	58	al	
D	4	g2	o	83	al	
D	4	g2	o	82	al	
D	5	g1	m	63	cu	13.00
D	5	e	o	77	al	
D	5	m1	m	72	al	
D	5	m2	m	59	al	
D	5	m2	o	77	al	
D	5	m1	m	72	al	
D	5	e	m	67	al	
D	5	g2	o	82	al	
D	5	g1	m	62	fg	
D	5	e	o	77	al	
D	5	m1	m	72	al	
D	5	m2	m	59	sc	19.00
D	5	m2	o	77	al	
D	5	m1	m	72	al	
D	5	e	m	67	og	17.50
D	5	g2	m	62	al	
D	5	g1	m	59	al	
D	5	e	m	70	sc	21.00
D	5	m1	m	72	al	
D	5	m2	m	61	al	
D	5	m2	o	77	al	
D	5	m1	m	72	al	
D	5	e	m	63	al	
D	5	g2	m	73	og	17.00
D	5	g1	m	59	al	
D	5	e	m	70	al	
D	5	m1	m	72	al	
D	5	m2	m	61	al	
D	5	m2	o	77	al	
D	5	m1	m	54	ha	12.50
D	5	e	m	59	sc	20.00
D	5	g2	m	73	al	
D	5	g1	m	59	al	

B	8	m2	o	90	sc	14.50
B	8	m2	m	70	al	
B	8	g2	m	69	al	
B	8	g1	m	86	al	
B	8	m1	o	87	al	
B	8	m2	m	75	al	
B	8	m2	m	70	al	
B	8	g2	m	69	fg	
B	8	g1	m	86	al	
B	8	e	m	73	fg	
B	8	m1	o	87	al	
B	8	m2	m	75	al	
B	8	m2	m	70	al	
B	8	g2	m	62	al	
B	8	g1	m	72	fg	
B	8	e	m	64	al	
B	8	m1	o	87	al	
B	8	m2	m	75	al	
B	8	e	m	70	al	
B	8	g2	m	62	al	
B	8	g1	m	83	hg	
B	8	e	m	64	fg	
B	8	g2	o	87	al	
B	8	g1	m	75	hg	
B	8	e	m	70	og	17.00
B	8	g2	m	62	hg	
B	8	g1	m	71	og	16.00
B	8	e	m	70	sc	11.50
B	8	g2	m	82	al	
B	8	g1	m	75	at	
B	8	m1	m	86	sc	16.00
B	8	m1	o	92	al	
B	8	m1	m	78	al	
B	8	m1	o	92	sc	.
B	8	e	m	78	al	

D	5	e	m	58	at	
D	5	m1	m	72	al	
D	5	m2	m	61	al	
D	5	m2	m	63	al	
D	5	m1	m	54	al	
D	5	e	m	59	al	
D	5	g2	m	64	og	16.50

Appendix F: Raw data from the Patch Shape Study (Chapter 4)

Patch #	Depth (m)	Visual Estimate Area @4m^2	Fractal minimization	Fractal fixed	# eaten	total set	fraction eaten
1	5.7912	12	1.2849	1.3788	8	8	1.00
2	6.7056	22	1.2219	1.2087	6	7	0.86
3	7.3152	2	1.4034	1.4041	4	7	0.57
6	7.0104	1	1.4015	1.4769	6	6	1.00
8	6.7056	6	1.2621	1.3053	4	8	0.50
10	7.0104	7.5	1.2952	1.3355	2	8	0.25
11	6.7056	1	1.3515	1.3515	1	9	0.11
12	6.4008	80	1.4407	1.4674	2	8	0.25
14	5.1816	15	1.2911	1.3083	3	8	0.38
15	5.1816	2	1.3414	1.3818	7	7	1.00
16	5.1816	3	1.2628	1.2691	7	8	0.88
17	5.4864	6	1.36	1.366	3	8	0.38
19	5.4864	70	1.4317	1.4433	2	7	0.29
20	5.4864	24	1.3423	1.3575	5	9	0.56
21	5.7912	4	1.2794	1.3104	7	8	0.88
22	5.4864	20	1.3463	1.3731	7	8	0.88
23	5.4864	64	1.4137	1.4771	6	8	0.75
25	5.1816	6	1.268	1.2729	5	7	0.71
27	6.7056	35	1.3719	1.4221	8	8	1.00
28	6.7056	16	1.3245	1.2495	6	8	0.75
29	6.4008	26	1.335	1.3604	3	8	0.38
30	5.7912	48	1.3609	1.3651	5	6	0.83
32	6.096	40	1.3142	1.3717	6	7	0.86
34	7.3152	6	1.2476	1.3077	6	8	0.75
35	6.7056	4	1.3146	1.3637	5	8	0.63