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Regional variation in fish predation intensity: a historical perspective in the Gulf of Maine

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Summary. Regional variation in the intensity of fish predation on tethered brittle stars and crabs was measured at 30–33 m depths in the rocky subtidal zone at seven sites representing coastal and offshore regions of the Gulf of Maine, USA. Analysis of covariance comparing the slopes of brittle star survivorship curves followed by multiple comparisons tests revealed five groupings of sites, with significantly greater predation rates in the two offshore than in the three coastal groups. Brittle stars tethered at the three offshore sites were consumed primarily by cod, *Gadus morhua,* with 60–100% prey mortality occuring in 2.5 h. In striking contrast, only 6–28% of brittle star prey was consumed in the same amount of time at the four coastal sites, which were dominated by cunner, *Tautogolabrus adspersus.* In several coastal trials, a majority of brittle star prey remained after 24 h. The pattern of higher predation offshore held for rock crabs as well with only 2.7% of tethered crabs consumed ($n = 36$) at coastal sites versus 57.8% of crabs ($n = 64$) consumed at offshore sites. Another important predatory fish, the wolffish, *Anarhichas lupus,* consumed more tethered crabs than brittle stars. Videos and time-lapse movies indicated that cod and wolffish were significantly more abundant at offshore than at coastal sites. Three hundred years of fishing pressure in New England has severely depleted stocks of at least one important benthic predator, the cod, in coastal waters. We speculate that this human-induced predator removal has lowered predation pressure on crabs and other large mobile epibenthos in deep coastal communities. Transect data indicate that coastal sites with few cod support significantly higher densities of crabs than offshore sites with abundant cod.

Key words: Regional variation – Rocky subtidal – Predator-prey interactions – Overfishing – Human impact

The ecological and evolutionary impact of predation varies on local (meters to few kilometers), regional (100's of kilometers) and geographical (1000's of km) spatial scales. Manipulative field experiments conducted on the local spatial scale have contributed two predictions providing a conceptual basis for understanding predator impact in different habitats; 1) predation intensity decreases along gradients of increasing environmental harshness (Connell 1975; Menge and Sutherland 1976, 1987; Menge and Olson 1990) and 2) the risk of predation is reduced by biogenic or physically generated refuges (Menge 1976; Woodin 1978; Heck and Thoman 1981; Menge and Lubchenco 1981; Peterson 1982; Watanabe 1984; Witman 1985). In addition, alternate "states" of marine benthic communities can result from localized differences in predation (Sebens 1986; Barkai and McQuaid 1988). Probably due to the logistical difficulty of conducting field experiments at many widely separated sites, few studies of variation in predation intensity or impact have been conducted in marine benthic communities at regional spatial scales. By documenting the results of a natural predator removal event, Estes et al. (1978) attributed large differences in kelp forest community structure among the Aleutian Islands to regional variation in predatory control of sea urchins by sea otters. To our knowledge, the sole experimental study of regional variation in consumer pressure was conducted by Hay (1984), who suggested that the role of herbivorous fish in structuring Caribbean reef communties has been underemphasized because most studies of herbivory were conducted on overfished reefs. On the larger geographical scale, Dethier and Duggins (1989) demonstrated that a herbivorous chiton controlled intertidal algal diversity on the coast of Washington, but not at the northern limit of it's distribution in Alaska. Differences in the shell morphology of intertidal gastropods between biogeographical regions led Vermeij (1976, 1978) to hypothesize that the stronger shell sculpture and smaller apertures of tropical gastropods evolved in response to greater predation intensity in the IndoPacific than in tropical Atlantic provinces. Experimental tests of latitu-

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dinal differences in predation pressure have indicated a higher incidence of shell crushing predation in the tropics (Panama) than in the temperate zone (Massachusetts; Bertness et al. 1981). A well replicated study by Heck and Wilson (1987) demonstrated that predation on brachyuran crabs living in seagrass beds was higher in tropical (Bermuda) than in similar temperate habitats in New Jersey.

Local marine benthic ecosystems are linked on the larger regional spatial scale by events in the overlying water column such as advective transport of food and larvae, internal waves and stratified fronts (Denman and Powell 1984; Wolanski and Hamner 1988). Determining the extent to which local sites are coupled or de-coupled to such regional processes is critical to the development of regional models of community structure (Roughgarden et al. 1988) and is possibly the most important challenge of modern ecology (Dayton and Tegner 1984; Ricklefs 1987). Since predatory fish can alter the composition of temperate subtidal benthic communities (Choat 1982; Cowen 1983; Aronson 1989), overfishing of important predatory fish at local sites could be a major determinant of variation in subtidal benthic community structure on the regional level. We provide the first experimental evidence that fish predation intensity varies predictably on the scale of hundreds of kilometers distance in rocky subtidal communities.

Patterns of predation intensity and fish abundance were documented at four coastal and three offshore rocky ledges in the Gulf of Maine. Fish abundance alone was measured at a fourth offshore ledge (Table 1, Fig. 1).The main question addressed was: does predation intensity, defined as the rate of prey consumption in a given habitat (Menge 1978), differ between coastal and offshore regions of the Gulf of Maine? Insight into community-level influences of fish predation were provided by fish diet information and comparative data on the abundance of some fish prey (mobile epibenthos) at all sites. Research cruises were conducted during the summers of 1987–1990 to replicate predation trials at the seven widely spaced sites, since it was not feasible to conduct replicate experiments at all sites simultaneously.

Methods

The Gulf of Maine is a an attractive system in which to investigate regional variation in ecological processes affecting rocky subtidal communities because it is a large, semi-enclosed, basin containing hundreds of rocky islands and many subtidal ledges to serve as site replicates. Replicate sites become more limited, however, with distance from shore because the offshore ledges are relatively deep ($\geq$30 m, with one exception). To eliminate bathymetric influences on fish predation in this study, all sites were located at 30–33 m depth. The transition between the rocky inner shelf margin and the outer shelf basin of the Gulf of Maine occurs at 60–90 m depth (Belknap et al. 1988). Thus, we consider the 100 m depth contour to be the boundary between the coastal and offshore regions of the Gulf (Fig. 1) because it is seaward of the inner shelf margin. Most of the offshore sites are separated from the coastal sites by deep sedimentary basins, with the exception of Pigeon Hill, an isolated rocky knoll offshore on Jeffreys Ledge.

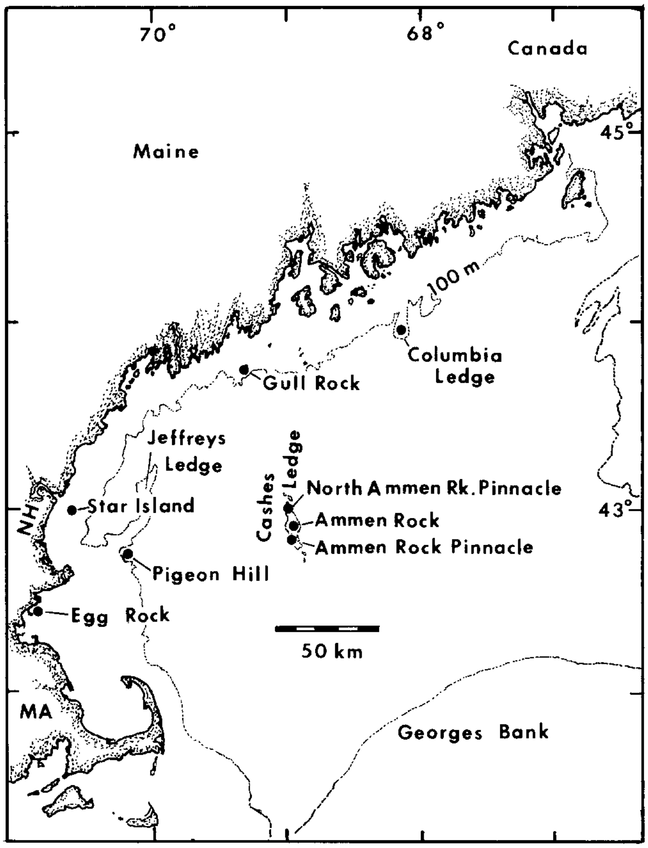

Fig. 1. Map of the Gulf of Maine showing the location of rocky subtidal sites where the predation intensity experiments and photographic estimates of fish abundance were conducted. Dotted line represents the 100 m isobath delineating coastal and offshore regions

Predation intensity and fish abundance

Rates of prey consumption and the abundance of cod, cunner, wolffish and flounder were recorded by time-lapse 8 mm movie cameras and by 8 mm video cameras focused on benthic invertebrate prey (brittle stars *Ophiopholis aculeata;* or crabs: *Cancer irroratus, C. borealis*) tethered to small chains placed on the sea floor by divers. Brittle stars and crabs are part of the natural diet of these fish (Bigelow and Schroeder 1953; Hacunda 1981; Langton 1982; Ojeda 1987). All predation experiments were conducted on nearly flat areas of bedrock in "open" sparsely vegetated habitats. In a few instances where kelp was abundant at a designated site, it was cleared ($\sim$40 m^{-2} area) two to three days prior to the experiment to standardize habitat type across all sites. This was necessary because all coastal sites lacked kelp at the 30–33 m study depth. Consequently, the predation rates reported here should be regarded as an estimate of maximum predation intensity because the predation experiments were conducted in exposed habitats lacking the spatial refuge of dense vegetation (Heck and Thoman 1981; Summerson and Peterson 1984; Watanabe 1984). Such "open" habitats are typical of deep rocky ledges of the Gulf of Maine (Sears and Cooper 1978; Hulbert et al. 1982; Witman 1985; Witman and Sebens 1988).

The protocol for the predation experiments consisted of placing two 1 m lengths of steel link chain with tethered prey (brittle stars or crabs) on the bottom approximately 1.5 m in front of the movie and video cameras. The discs of brittle stars were pierced with a fine needle and a knot was tied around the disc with fine monofilament. Six brittle stars were then tied to each chain so they were on 15–20 cm monofilament tethers, for a total of 12 prey per trial. No brittle stars died as a result of the tethering procedure. A previous

Table 1. Characteristics of predation intensity experiments and non-experimental deployment of video and time-lapse movie cameras to record fish abundance in deep rocky subtidal habitats of the Gulf of Maine. Most of the trials with tethered crabs in the coastal zone were monitored directly by SCUBA diving due to the low predation rates there. Site codes are listed below or adjacent to site names. Trial numbers abbreviated as t1 for trial 1, etc. Site codes and trial numbers are combined to specify data in figures and tables

Site	Location (Lat./Long.)	Distance from coast (km)	Trial No.	Date	Duration of video (V) or movie (M) in minutes	Number of movie frames analyzed
Offshore sites: Predation trials						
Brittle star prey						
Ammen Rock Pinnacle (ARP)	42° 51.25′ N, 68° 57.11′ W	103	1	7/18/87	51 V/1375 M	917
			2	9/3/87	86 V/1545 M	1030
			3	9/6/87	79 V/1146 M	764
			4	9/7/87	77 V/2053 M	1369
Ammen Rock (AR)	42° 52.96′ N, 68° 56.32′ W	96	1	7/13/87	80 V/945 M	630
North Ammen Rock Pinnacle (NARP)	42° 55.20′ N, 68° 57.59′ W	100	1	6/29/90	85 V	
			2	6/29/90	80 V	
			3	7/18/90	90 V	
			4	8/12/90	88 V	
Crab prey						
Ammen Rock Pinnacle	(as above)	103	1	6/19/87	86 V/–	
			2	6/20/87	72 V/1815 M	1210
			3	7/10/87	69 V/–	
			4	6/18/88	60 V/1342 M	895
			5	6/19/88	60 V/1291 M	861
			6	6/20/88	61 V/3190 M	2127
			7	8/12/88	71 V/2904 M	1936
			8	8/14/88	–/2140 M	1427
North Ammen Rock Pinnacle	(as above)		1	8/20/89	observation	
			2	8/20/89	75 V	
			3	8/21/89	85 V	
Offshore sites: Ambient cameras						
Ammen Rock Pinnacle	42° 51.25′ N, 68° 57.11′ W	103		6/21/87	–/1460 M	973
				7/10/87	–/2650 M	1767
Pigeon Hill (PH)	42° 46.6′ N, 70° 14.5′ W	37		7/12/87	55 V/–	
				7/28/87	75V/–	
Coastal sites: Predation trials						
Brittle star prey						
Columbia Ledge (CL)	43° 57.5′ N, 68° 7.0′ W	29	1	7/17/87	57 V/534 M	356
			2	7/17/87	67 V/300 M	200
Gull Rock (GR)	43° 45.0′ N, 69° 17.5′ W	19.5	1	7/15/87	61 V/396 M	264
			2	7/15/87	60 V/1299 M	866
Star Island (SI)	42° 58.45′ N, 70° 36.90′ W	10	1	8/2/87	90 V/2973 M	1982
			2	8/7/88	62 V/1410 M	940
Egg Rock (ER)	42° 25.89′ N, 70° 53.57′ W	1.6	1	8/20/87	60 V/4017 M	2678
			2	8/13/88	60 V/600 M	400
Crab prey						
Gull Rock	43° 45.0′ N, 69° 17.5′ W	19.5	1	6/24/87	observation	
			2	6/22/88	observation	
Star Island	42° 58.45′ N, 70° 36.90′ W	10	1	7/22/87	–/1560 M	1040
			2	8/10/87	observation	
Egg Rock	42° 25.89′ N, 70° 53.57′ W	1.6	1	8/21/87	observation	
			2	8/23/87	observation	

experiment at one of the coastal sites indicated that tethered brittle stars do not incur artificially high predation rates due to the attraction of chemosensory predators (Witman 1985). Two to five brittle star trials were performed at each site (Table 1). One trial at North Ammen Rock Pinnacle (NARP) was rejected when a large sea star moved onto the chain and obscured the prey. The mean sizes of brittle stars used in the coastal and offshore predation experiments did not differ (1.31 cm ± 0.45 (SD), vs 1.23 cm ± 0.30 (SD) $F = 2.1$, 1, 202 df, $P > 0.05$, one way ANOVA, data log transformed). Crabs were tethered by drilling a one mm diameter hole through the thin edge of the carapace (thus not piercing the body cavity) at its broadest point so that a 20–30 cm length of heavy monofilament could be tied to the carapace and to the chain. Six trials with tethered crabs were performed in the coastal zone and eleven on offshore ledges, with a minimum of two replicate trials per site (Table 1). In most cases three crabs were tethered to each chain, and the trial was conducted with six crabs. Exceptions occurred in the first and second trials performed at Ammen Rock Pinnacle (ARP) in 1987 when seven crabs were tethered, and when trial 3 at ARP was conducted with three crabs in 1988. The average carapace width of crabs used in offshore trials (5.40 cm ± 0.81 SD, $n = 64$) was not significantly different from the carapace width of crabs in coastal trials (5.44 cm ± 0.94 cm SD, $n = 36$; one way ANOVA, $F = 1.4$, df = 1, 99, $P > 0.05$, data log transformed). Most of the coastal crab trials were monitored by SCUBA diving rather than by time-lapse photography because pilot experiments indicated that rates of predation on crabs were extremely low in the coastal zone.

The time lapse movie system designed for this study consisted of a Minolta 8 mm movie camera equipped with an intervalometer. Flash illumination was provided by a mini-strobe hard wired to the camera. The movie camera exposed frames at 1.5 min intervals for 2–3 days while a video camera (Sony "Handycam"™ in an AquaVision "Capsule 8"™ housing) recorded continuously the initial 80–90 min of the experiments. Predation trials at North Ammen Rock Pinnacle were videotaped with a Sony V99 ™ 8 mm camcorder in a HyperTech™ housing. Predation attacks and the number of fish visiting the experimental areas were counted from the videos and movie film. On two occaisions movie cameras were set down at Ammen Rock Pinnacle without tethered prey to record "ambient" numbers of fish for comparison to fish abundances recorded during the experiments (Table 1). Care was taken in counting fish from video tapes to distinguish individual fish and to separate them from a return visit by the same fish. While this procedure worked for the videos, it was not always possible to separate individual fish in the movies. Consequently, we refer to the estimate of fish abundance based on the time lapse movies as the number of fish "visits" per day.

Line transects were used to quantify the abundance of rock crabs *(Cancer borealis* and *Cancer irroratus)* at four coastal and three offshore sites. The procedure consisted of dropping a ten-meter long transect line onto nearly horizontal areas of bedrock and stretching out the line in a compass bearing previously chosen from a random number table (method of Witman 1985). Divers then swam the length of the line to count all crabs within a 1.0 meter wide swath, yielding an estimate of density per 10.0 m^{-2}. Four replicate transects were surveyed at each site.

Statistical analyses

The null hypothesis that rates of predation on tethered brittle stars did not differ among sites was tested by comparing linear regressions of the number of brittle stars surviving (y) vs time in minutes (x) by analysis of covariance (ANCOVA). A regression line was computed for each brittle star trial in Table 1. The slopes of these regression lines were compared since they represent the actual predation rate. Values of the dependent variable were $\log_{10}(y+1)$ transformed to satisfy the assumption of ANCOVA that y scores are normally distributed (Huitema 1980). Where slopes were significantly different, a Tukey multiple comparisons test (Zar 1981) was used to compare slopes, determining which predation trials differed. The ANCOVA was run on 17 regression lines (trials) in one bulk analysis. Thus, a site-wide pattern in predation rate was identified by the lack of significant differences among the slopes of regression lines representing replicate trials from the same site. Similar use of ANCOVA to compare mortality rates were reported by Moran et al. (1984) and Etter (1989).

Several research cruises were needed during June–August 1987, 1988, 1989 and 1990 to repeat the predation trials at the seven widely spaced sites. Since it was not feasible to achieve a completely balanced sampling design with trials conducted at all sites simultaneously, the possibility of identifying an explicit regional spatial pattern was compromised by the inclusion of temporal (interannual) variation in the analysis. However, only one site showed significant interannual variation in fish predation intensity (Table 2).

Table 2. The results of analysis of covariance and a Tukey multiple comparison test comparing the slopes of regression lines fit to prey survivorship. The slope represents the rate of prey (brittle stars) consumption. The multiple comparisons indicate which trials differed significantly ($p < 0.05$). Trials separated by a single inequality sign (>) were significantly different at $p < 0.05$, with the sign indicating the direction; sites separated by two inequality signs (≫) differed at $p < 0.001$, sites separated by a comma did not differ. * $p < 0.05$, ** $p < 0.025$, *** $p < 0.001$. ns = non-significant

Site & Trial	Regression			Ancova			Tukey Multiple Comparisons
	Equation	df	F	Parameter	df	F	
Log (y+1) no. of prey (y) vs time in min. (x)							Ranking of Sites/Trials
ARP t1	$y = 1.186 - 0.0061x$	1,9	29.91***	Slope	16, 101	41.51***	AR, ARP t2, ARP t3, NARP t2,
ARP t2	$y = 1.169 - 0.0196x$	1,9	69.57***	Elevation	16, 117	2.14*	NARP t1 > NARP t3, NARP t4, ARP t1,
ARP t3	$y = 0.988 - 0.0180x$	1,7	419.05***				ARP t4 ≫ ERt2 > CL t2, GR t2, CLt1,
ARP t4	$y = 1.132 - 0.0044x$	1,7	56.31***				GR t1 > SI t2, ER t1, SI t1
AR	$y = 1.164 - 0.0228x$	1,5	66.65***				
NARP t1	$y = 1.131 - 0.0122x$	1,7	36.71***				
NARP t2	$y = 1.142 - 0.0123x$	1,10	52.56***				
NARP t3	$y = 0.984 - 0.0088x$	1,8	28.83***				
NARP t4	$y = 1.124 - 0.0074x$	1,9	88.58***				
CL t1	$y = 1.061 - 0.0004x$	1,3	12.84*				
CL t2	$y = 1.078 - 0.0008x$	1,4	11.75*				
GR t1	$y = 1.039 - 0.0001x$	1,5	7.38*				
GR t2	$y = 1.040 - 0.0006x$	1,11	113.58***				
SI t1	$y = 1.096 - 0.00002x$	1,4	2.83 ns				
SI t2	$y = 1.072 - 0.00005x$	1,6	7.78*				
ER t1	$y = 1.099 - 0.00004x$	1,4	7.76*				
ER t2	$y = 1.061 - 0.0015x$	1,11	192.80***				

Site-specific differences in the average abundance of fish were compared by a Kruskal Wallis test followed by Dunn's multiple comparisons tests (Zar 1981).

Results

The general pattern revealed by analysis of covariance followed by multiple comparisons of regression line slopes was that the intensity of predation on the tethered brittle stars was significantly higher at offshore than at coastal sites (Table 2, Fig. 2). Multiple comparisons segregated predation trials into five groupings including two offshore groups characterized by high predation intensity, and three coastal groups of low predation intensity. Differences between regions were highly significant ($p < 0.025$, Table 2) with the separation of offshore vs coastal trials occurring between Ammen Rock Pinnacle (ARP) trial 4 and Egg Rock (ER) trial 2. The magnitude of the differences was striking; 60–100% of tethered brittle stars was consumed by fish in 2.5 h in a total of nine trials at three offshore sites, whereas only 6–28% of the prey was eaten in the same amount of time in a total of eight trials in the coastal region (Fig. 2). Cod, *Gadus morhua,* accounted for 94.0% of the total number of predation attacks on brittle stars ($n = 99$) witnessed offshore, while the remaining 6.0% was by wolffish, *Anarhichas lupus.* In contrast, only 7.5% of the total number of predation attacks filmed at the coastal sites was by cod and 92.5% of the attacks was by cunner, *Tautogolabrus adspersus.* The few cod predation attacks recorded in the coastal region occurred at Gull Rock ($n = 1$) and Columbia Ledge ($n = 2$). There was significant temporal variation in predation intensity at Egg Rock between 1987 (ER t1) when it was low, and 1988 when it was higher (ER t2), as revealed by the Tukey multiple comparisons tests following ANCOVA (Table 2).

Rock crabs were consumed more slowly than brittle stars, but the spatial pattern of fish predation on tethered crabs, *Cancer irroratus* and *C. borealis,* was similar with higher predation at offshore than at coastal sites (Fig. 3). Only one *Cancer irroratus* was eaten (Gull Rock, June 1988) in six 48 h trials performed at the coastal sites. In comparison, all crabs were eaten in three of eleven trials conducted offshore, with 17–60% of the crabs consumed in 15–36 h in the other eight offshore trials (Fig. 3). Wolffish contributed more to offshore prey mortality in the crab trials than in the brittle star trials, accounting

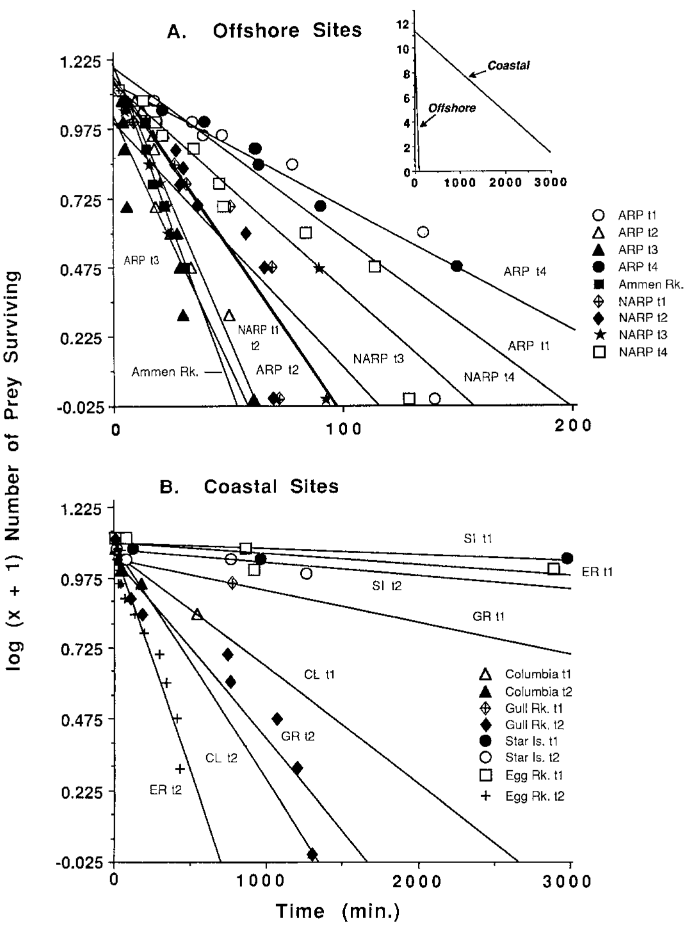

Fig. 2. Survivorship of tethered brittle stars, *Ophiopholis aculeata,* in predation experiments at offshore (**A**) and coastal (**B**) study sites. Site and trial abbreviations are listed in Table 1. Linear regression analysis was performed on each trial; regression equations are presented in Table 2. The slopes of the regression lines indicate the actual predation rate. Regression lines from NARP trials 1 and 2 are nearly identical. Inset at upper right shows summarized regression lines (all data pooled by region) plotted on same y axis for comparison. Multiple comparisons of slopes following ANCOVA revealed significantly higher rates of brittle star consumption offshore. All regression lines passed through the same number initially, 1.114, representing the $\log_{10}$ (x+1) transform of 12 brittle stars. Cod predation accounted for 94%, and wolffish predation 6%, of brittle star mortality in trials offshore while cunner were responsible for 92.5% and cod 7.5% of brittle star mortality in coastal trials

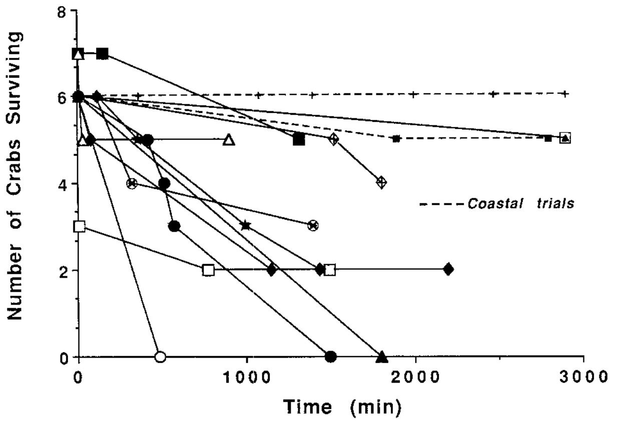

Fig. 3. A comparison of the survivorship of tethered crabs *(Cancer irroratus* or *Cancer borealis)* in predation experiments between coastal and offshore regions. Horizontal dashed line is a composite of data from 5 coastal sites (SI t2, GR t1, ER t1, ER t2), illustrating no prey mortality. The only predation in any of the coastal trials is depicted in the lower dashed line where one crab was consumed at Gull Rock (t2). All other survivorship lines are from offshore trials conducted at 30 m depth. Legend to these offshore trials is ARP t1 = lg. black square, ARP t2 = open triangle, ARP t3 = black triangle, ARP t4 = open circle, ARP t5 = solid circle, ARP t6 = open square, ARP t7 = small black triangle within square, ARP t8 = cross within diamond, NARP t1 = solid diamond, NARP t2 = star, NARP t3 = x within circle. Crabs were eaten by wolffish in ARP t3, ARP t4, NARP t1 and by cod in ARP t2, ARP t5, and ARP t8

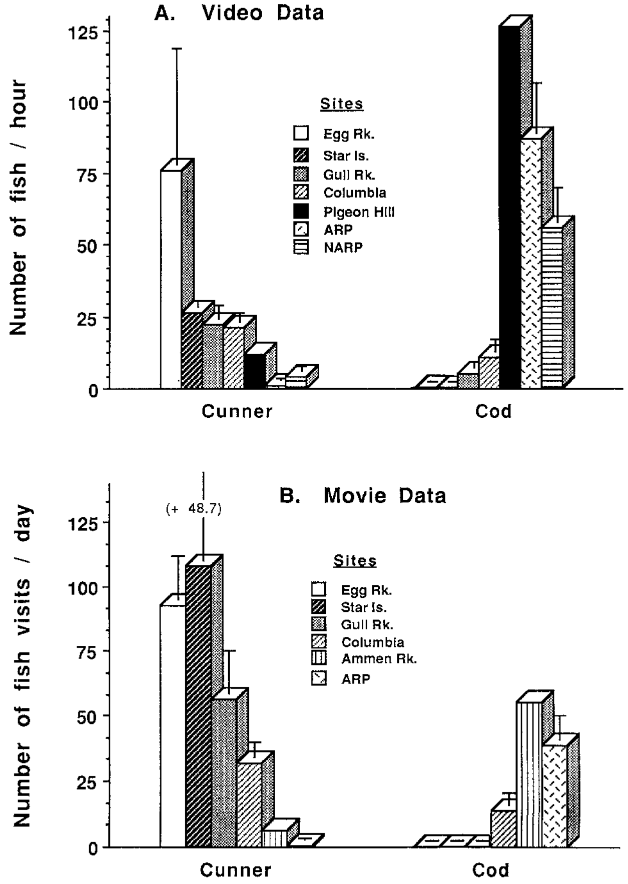

Fig. 4A, B. Average cunner *(Tautogolabrus adspersus)* and cod *(Gadhus morhua)* abundance at sites (30–33 m depth) generally arranged with increasing distance from shore along x axis for each fish species (ARP, AR, and NARP are nearly the same distance), based on 75–90 min deployment of video cameras (**A**) and time-lapse movies taken at 1.5 min intervals (**B**). Error bars are standard errors with $n=2$ for all coastal sites (video & movie), $n=4$ for ARP video and movie, and $n=4$ for NARP video. Only 1 sample available from Pigeon Hill and Ammen Rock sites. Video cameras covered approximately 2.2 m^{-2} area of the bottom, whereas the area covered by the movie cameras was 0.31 m^{-2}

for all predation on crabs in two out of eleven trials (ARP t3, ARP t4) and in one predation event directly witnessed by divers at North Ammen Rock Pinnacle (NARP t1). Crabs in three of the trials (ARP t2, ARP t5, ARP t8) were consumed by cod. Although predators were not photographed by the movie cameras in the other five trials, predators were clearly responsible for prey mortality because crushed crab remains were found tied to the chains at the end of the experiments.

Further evidence of greater predation intensity offshore resulted from a reciprocal mussel growth experiment that was ruined by fish predation. Thirty large horse mussels, *Modiolus modiolus,* were transplanted from 30 m depth at a coastal site (Gull Rock) to the same depth offshore on Ammen Rock Pinnacle and vice-versa to examine the influence of regional (coastal vs offshore) differences in phytoplankton food supply on mussel growth. The transplant technique consisted of embedding portions of individual mussels in small blobs of underwater epoxy in a linear array approximately 20–25 cm apart on the open rock surface away from physical substrate refuges or the protection of a mussel bed. All mussels transplanted to Ammen Rock Pinnacle were eaten when we returned forty nine days later on August 12, 1988, while no mussels were consumed at Gull Rock. Fragmented mussel shells were left on the epoxy pads used to attach them to the bottom. We suspect that wolffish were responsible for the predation because two large wolffish were observed near the crushed mussels, and *M. modiolus* are common prey of these shell-crushing fish (Jonsson 1982; Keats et al. 1986). Such inter-site differences in mussel mortality could not be explained by size-limited predation (*sensu* Paine 1976), because the mean shell lengths of *M. modiolus* transplanted offshore from Gull Rock to Ammen Rock Pinnacle (9.59 cm ± 1.44 SD) and vice-versa (10.15 cm ± 3.18 SD) did not differ (one way ANOVA, F = 0.74, df = 1,53, $p > 0.05$, log transformed data).

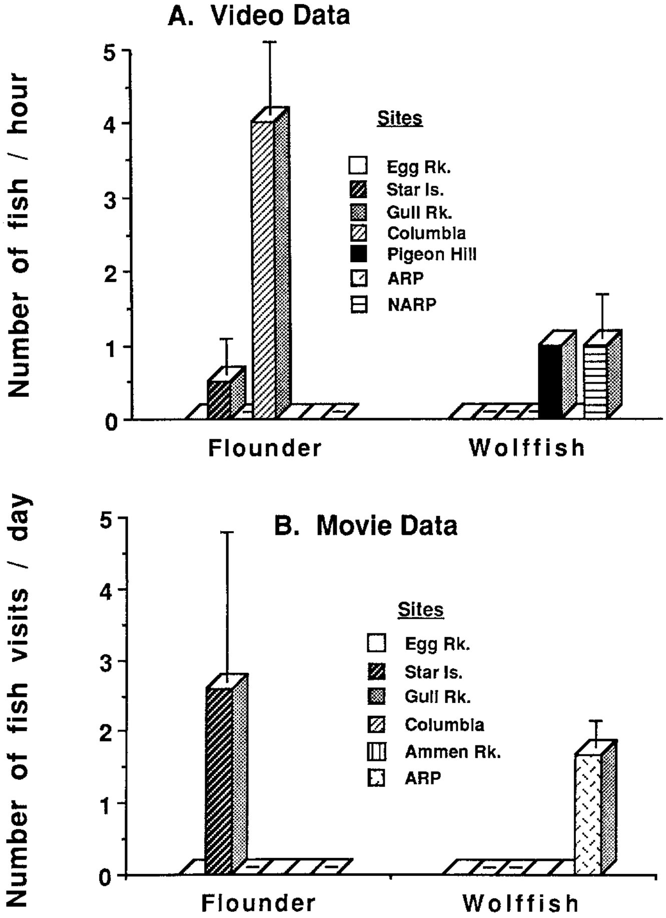

Fig. 5A, B. Average flounder *(Pseudopleuronectes americanus)* and wolffish *(Anarhichas lupus)* abundance at coastal and offshore sites. Error bars represent standard errors as in Fig. 4, with same sample sizes

Higher predation intensity at offshore sites is a function of the greater abundance of large predatory fish there (Figs. 4 and 5). Both video tapes and the longer term 2–3 day time lapse movies indicated that cod were significantly (Table 3) more abundant at offshore than at coastal sites. The movie data revealed significantly higher

Table 3. The results of Kruskal Wallis test and Dunn's multiple comparisons tests comparing fish abundance at 30 m depth at coastal and offshore sites (Figs. 4 and 5). Comparisons made only on sites where > 1 movie or video recording was conducted. Sites separated by an inequality sign were significantly different with the sign indicating the direction

Fish	Kruskal Wallis		Dunn's Multiple Comparisons		
	H	v	Q	k	Ranking of Sites
Movie Data					
Flounder	11.9*	4	5.06***	5	SI > ER, GR, CL, ARP
Wolffish	10.5*	4	2.87*	5	ARP > SI, ER, GR, CL
Cunner	13.0**	4	2.82*	5	ER, SI, GR, CL > ARP
Cod	12.2**	4	4.86***	5	ARP > ER, SI, GR, CL
Video Data					
Flounder	17.3***	5	4.60***	6	CL, SI > GR, ER, ARP, NARP
Wolffish	17.1***	5	9.49***	6	NARP > ARP, CL, GR, SI, ER
Cunner	18.2***	5	5.50***	6	ER, SI, GR, Cl > ARP, NARP
Cod	17.8***	5	35.0***	6	ARP, NARP > ER, SI, GR, CL

* $p<0.05$, ** $p<0.025$, *** $p<0.001$

Table 4. Comparison of crab densities (*Cancer* spp.) at 30 m depth in coastal and offshore rocky subtidal habitats. Data represent mean densities ($\bar{x}$) per 10 m^2, n = four replicate 10 × 1 m band transects per site, with standard errors (SE). One way ANOVA on log $(x+1)$ data indicated a significant difference among sites ($F=5.62$, $p=0.0013$, 6,21 df). Fisher's least significant difference test indicated sites ER (= HR, SI, GR) > ARP, AR, NARP; $p<0.05$

	Coastal				*Offshore*		
	Halfway Rock	Egg Rock	Star Is.	Gull Rock	Ammen Rock Pinnacle	Ammen Rock	North Ammen Rock Pinnacle
$\bar{x}$	0.50	1.25	1.25	0.25	0	0	0
SE	0.28	0.25	0.47	0.25	0	0	0

Table 5. Stomach contents of cod caught by hook and line fishing at two offshore sites, Ammen Rock Pinnacle in June–July 1987 ($n=21$ stomachs) and Pigeon Hill in June–July 1984 ($n=50$ stomachs). Data expressed as the percent frequency of the prey item in all stomachs examined. Because more than one prey type could occur in one stomach, total percentages may exceed 100%. The crab prey category included both *Cancer borealis* and *C. irroratus*. – indicates item not present

Prey item	*Ammen Rock Pinnacle* Frequency	*Pigeon Hill* Frequency
Crabs	57.2	30.0
Ophiopholis aculeata	38.1	80.0
Unidentified fish	33.3	–
Polychaetes	9.6	82.0
Amphipods	14.3	74.0
Metridium senile	9.5	–
Stronglyocentrotus droebachiensis	–	4.0
Bivalves	–	2.0

wolffish abundance offshore (Table 3, Fig. 5). The greatest abundance of cod occurred at Ammen Rock Pinnacle where up to 226 cod were recorded in an hour, with an average of 86.6 cod/h (Fig. 4A). Pigeon Hill, an offshore site on Jeffreys Ledge, ranked second with 126 cod/h in the single video recording conducted there. Large numbers of cod were also recorded from the third offshore site, North Ammen Rock Pinnacle (Fig. 4A). Fish abundance patterns did not appear to be an novelty artifact associated with tethered prey because the average number of cod visits/day recorded by two "ambient" movie cameras at Ammen Rock Pinnacle (40.8 ± 6.5 SD, $n=2$) did not differ from the number of cod visits/day recorded by movie cameras during the brittle star and crab trials performed at ARP in the summer of 1987 (41.4 ± 25.0 SD, $n=7$; $U=5$, $n=9$, $p>0.05$, Mann Whitney U test). Cunner replaced cod as the most abundant demersal fish at deep coastal sites, and were especially numerous at Egg Rock and Star Island (Table 3, Fig. 4). Cunner are common at the one shallow ledge offshore (15 m, Ammen Rock), but their densities decline sharply with depth (J. Witman and K. Sebens, unpublished data). Short term estimates of cod and cunner abundance based on the video cameras were substantially higher than daily estimates of fish visits obtained by the movie cameras (eg. compare Fig. 4A vs B) reflecting differences between the continuous (video) and interval (time-lapse movie) recording modes, and the seven fold larger area of the bottom covered by the wide angle video cameras (2.2 m^{-2} video vs 0.31 m^{-2} area viewed by movie cameras). Both methods, however, revealed similar spatial patterns of cod and cunner abundance.

Line transect data indicated that densities of rock crabs were significantly lower at Ammen Rock Pinnacle, Ammen Rock and North Ammen Rock Pinnacle than at four coastal sites (Table 4). Stomach contents of 71 large cod caught by hook and line fishing at two offshore sites, Ammen Rock Pinnacle on Cashes Ledge and Pigeon Hill on Jeffreys Ledge, indicated that rock crabs were an important component of their diets at these sites (Table 5).

Discussion

Fish predation risk for benthic invertebrates varies on the small spatial scales characteristic of biogenic (eg. mussel beds, Witman 1985) and physical (cobble, Wahle 1988, 1990) refuges in the rocky subtidal zone of the Gulf of Maine. Using a standard "open" habitat (eg. non –

refuge) on horizontal rock substrata as a basis of comparison, we provide the first evidence for this region that fish predation intensity varies consistently on a considerably larger scale, on the order of 100 kilometers, with distance from the coast.

Although it is an untestable hypothesis, we suggest that human exploitation of coastal fish populations is responsible for the observed pattern of greater fish predation intensity and greater abundance of large fish in offshore benthic ecosystems of the Gulf of Maine. The cod fishery began on the many small ridges and ledges in coastal waters of the Gulf, and was the first commercial enterprise of colonial New England (Innis 1940). Describing the plenitude of coastal cod in 1600–1630, Captain John Smith wrote "he is a very bad fisher who cannot kill in one day one, two or three hundred cod, which dressed and dried be sold for ten shillings a hundred" (Barbor 1986). New England fishermen were, however, greatly concerned about the depletion of nearshore fish stocks by the mid-1800s (Baird 1874). The fishery gradually moved to offshore banks such as Georges and Browns Banks throughout the later half of the nineteenth century (Jensen 1972; German 1987). Due to the persistence of an inshore fishery for cod, haddock and other demersal finfish in the Gulf of Maine, coastal groundfish stocks have never recovered from colonial times (Sette 1928; Rich 1929; Brown et al. 1978). Recently, Aronson (1990) has developed the paleobiological perspective that community changes brought about by shell crushing predators in the Mesozoic are analogous to recent effects of overfishing in that the influences of both phenomena began in the coastal zone.

Because all offshore predation experiments were conducted at three sites on Cashes Ledge, it is possible that the patterns we have described are not representative of true onshore-offshore differences, but rather reflect unusual features of this single, thirty-kilometer long ledge. Although we cannot completely discount this potential bias, our assertion that fish abundances at Cashes Ledge are typical of offshore regions of the Gulf of Maine is supported by our finding of abundant cod populations at another offshore site, Pigeon Hill on Jeffreys Ledge (Fig. 4). Fish predation intensity has not been measured at Pigeon Hill, but our research at Cashes Ledge indicates that cod abundance is a good predictor of cod predation intensity, thus we predict that fish predation intensity will also be high on Pigeon Hill. Furthermore, past studies have documented important influences of cod predation pressure on the benthos at Pigeon Hill (Witman and Cooper 1983). We have attempted to hold depth and topography constant in this study of regional variation, but we have been limited by the scarcity of rocky ledges or pinnacles at 30–40 m depths seaward of the coastal – offshore boundary. There are only four sites that qualify as discrete, rocky subtidal sites in the offshore region of the Gulf of Maine within safe SCUBA diving depths, and we have shown high abundances of large predatory fish at all of them (ARP, AR, NARP, PH), and high fish predation intensity at three out of the four sites. We cannot explain why large populations of cod and wolffish remain on offshore ledges in the central Gulf of Maine. We suspect, however, that the many peaks or pinnacles on Cashes and Jeffreys Ledge represent large spatial refuges from commercial fishing pressure because the rocky bottom topography at the tops of the ledges is too rough for bottom trawling. Moreover, we do not know why the large offshore cod populations do not migrate inshore to feed on the abundant crab populations in the coastal zone. Sparse populations of cod have been documented in the shallow subtidal (<20 m) zone at two coastal sites, Star Island (Witman 1985) and Pemaquid Point (Ojeda and Dearborn 1991), but cod densities have decreased since at the one site for which inter-annual data are available (J. Witman unpublished fish transects at Star Island, 10 m depth, 1987, 1988). The logistical difficulty of working in the central Gulf of Maine during the winter has hampered our ability to investigate seasonal variation in fish abundance or predation intensity. Our qualitative impression is that fish predation intensity and fish abundance in offshore regions is lower in the winter than in the summer when the experiments and observations were performed. For example, no cod were observed during four SCUBA dives at Ammen Rock Pinnacle in December 1989, and they have been relatively less common there and at North Ammen Rock Pinnacle during April 1989, 1990, 1991 than in late June of the same years (J. Witman, unpublished observations). Cod are still nearly absent during the winter at the coastal sites that we have studied (Star Island, Witman 1985; Halfway Rock, located 4.7 km NE from Egg Rock, 10 years unpublished observations by K. Sebens). If quantitative studies confirm our notion that fish predation pressure is lower during the winter than summer at offshore sites, then crabs and other large motile prey such as sea urchins that are readily consumed by cod (Table 5) and wolffish may have a temporal refuge from fish predation during the winter. The significant temporal variation in fish predation intensity observed at Egg Rock may have been caused by a greater consumption rate per individual cunner in the 1988 trial than in the 1987 trial, as cunner abundance at this site did not differ between years (Table 3).

The potential for spatial variation in fish predation intensity to explain onshore-offshore differences in the composition of deep rocky subtidal communities depends primarily on the diet of the fish, predator-prey size relations, on the extent to which other predators have replaced the missing ecological role of large predatory fish in coastal rocky subtidal communities, and the colonization dynamics of the benthic communities as a function of distance from shore. While the sessile invertebrate communities of relatively deep (30 m) coastal and offshore habitats are both composed of varying abundances of sponges, anemones, bryozoans and ascidians (Hulbert et al. 1982; Witman 1985; Vadas and Steneck 1988; Witman and Sebens 1988; Witman and Sebens 1990), large mobile epifauna such as cancrid crabs (*Cancer borealis* and *C. irroratus)* and sea urchins *(Strongylocentrotus droebachiensis)* are either scarce (Witman and Sebens 1988) or dominated by small size classes (urchins; Hulbert et al. 1982) at offshore sites. Differences in sessile invertebrate community structure throughout the Gulf of Maine regions are probably not directly influenced by spatial variation in fish predation because the sponges, anemones, bryozoans and ascidians comprising the structure of these communities are not commonly preyed upon by fish (Witman and Cooper 1983, T. Loher unpublished cod stomach data, but see Keats 1990 for Newfoundland). Working at an offshore knoll on Jeffreys Ledge, Witman and Cooper (1983) suggested that high cod predation on the biogenic substrata (polychaete tubes) used by juvenile brachiopods, *Terebratulina septentrionalis,* limited the abundance and influenced the size structure of populations living in "open" upper rock surface habitats at 33 m depth at Pigeon Hill. Given the remarkable spatial differences in predation intensity by large fish described in this study, the most obvious explanation for the scarcity of crabs at offshore sites is that their populations are regulated by cod and wolffish predation. Well replicated transects conducted on open expanses of horizontal bedrock showed that crabs were commonly encountered in these exposed habitats in the coastal zone, but were absent from them offshore. The only crabs we have seen in several hundred hours of diving between 1985–1991 at sites in the central Gulf of Maine (ARP, AR, and NARP) have been either hidden deep in cracks, crevices and cobble beds or were out at night (as revealed by two of the time lapse movies at ARP). We recognize that other factors such as the supply of crab larvae, the availability of crab food resources and the availability of physical refuges from fish predation may contribute to onshore – offshore differences in crab densities. There is, however, little evidence that the scarcity of crabs in offshore rocky habitats is due to recruitment failure as zoea larvae of cancrid crabs were collected during summer 1988 in a month-long experiment measuring larval supply at 29 and 35 m depth at two of the study sites on Cashes Ledge (J. Witman, unpublished data). Similar substrate relief (large expanses of horizontal – sloping bedrock) was one of the original criteria for the selection of the study sites, and it is unlikely that the availability of physical refuges differs greatly between sites.

Repercussions of crab population regulation by predatory fish in offshore communities may cascade down to lower trophic levels because *Cancer irroratus* and *C. borealis* are important consumers of mussels, barnacles, polychaetes, sea urchins and other bivalves (Elner 1980; Witman 1985; Sebens 1986; Ojeda and Dearborn 1991). Because of the comparatively small body size of the brittle star, *Ophiopholis aculeata,* it is vulnerable to predation from the entire spectrum of demersal fish from small – mouthed cunner to large wolffish. Thus, differences in *O. aculeata* abundances between coastal and offshore regions are not expected to result from fish predation because they are consumed by cunner at coastal sites and by cunner, cod and wolffish offshore. It is unlikely that cunner have "filled" the niche of the missing large predatory fish in coastal subtidal communites, because they are restricted to prey smaller than adult crabs (Ojeda 1987).

Whether removed gradually over hundreds of years by human exploitation, or removed abruptly in experimental manipulations, the absence of a keystone predator results in a shift to a different community composition (Paine 1966; Simenstad et al. 1978; Duggins 1980). Convincing evidence that a predator plays such a keystone role in a given community requires that the predator occurs in the habitat of the prey, that it actually consumes enough prey to regulate their populations, and that the community changes in the absence of the predator. The sea star, *Pisaster ochraceous* and the sea otter, *Enhydra lutris* are generally accepted as keystone predators in Pacific Northwest marine communities (Paine 1966; Levin 1988). Lobsters were considered to be keystone predators by controlling sea urchin populations in Northwest Atlantic subtidal communities (Breen and Mann 1976), but this hypothesis has recently come into question (Elner and Vadas 1990) because Vadas et al. (1986) showed that urchins do not form defensive aggregations in response to lobsters and lobster diet studies indicate that urchins are not a major food item (Elner and Campbell 1987). Human predation on keystone species (gastropods) has radically altered population and community structure in the rocky intertidal zone of Chile (Castilia and Duran 1985; Moreno et al. 1986). Because of their high predation rates, documented consumption of crabs, and the inverse relationship between crab and cod abundance, we suggest that cod are keystone predators directly regulating populations of cancrid crabs. Furthermore, we speculate that indirect trophic linkage effects (*sensu* Miller and Kerfoot 1987) of cod predation may impact populations of small epibenthos consumed by crabs (mussels, barnacles, polychaetes, small sea urchins, hiatellid bivalves) in deep offshore habitats of the Gulf of Maine. To advance beyond such correlative and circumstantial evidence will require experimental manipulation of cod densities.

This study illustrates the potential limitations of studying community processes at one or two local sites. Tethering experiments conducted within only one coastal or offshore region of the Gulf of Maine would lead to erroneous conclusions about the overall importance of fish predation in deep rocky subtidal communities. We argue that the currently successful experimental studies of benthic community dynamics at local sites should be placed into a context of variation on the regional level, because this spatial scale is large enough to encompass sites with varied histories of human-induced predator removal and varied exposure to oceanographic processes. Clearly, onshore-offshore differences in predation intensity within a region should be accounted for before comparisons of predation pressure are made between biogeographical regions.

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References

Aronson RB (1989) Brittlestar beds: low predation anachronisims in the British Isles. Ecology 70:856–865

Aronson RB (1990) Onshore-offshore patterns of human fishing activity. Palaios 5:88–93

Baird SF (1874) Conclusions as to decrease of cod fisheries on the New England coast. Report of the U.S. Commissioner of Fish and Fisheries for 1872 and 1873. Part 2: xi-xiv

Barbor PL (1986) The complete works of Captain John Smith. vol 1., University of North Carolina Press, Chapel Hill

Barkai A, McQuaid C (1988) Predator-prey role reversal in a marine benthic ecosystem. Science 242:62–64

Belknap DF, Kelley JT, Robbins DH (1988) Sediment dynamics of the nearshore Gulf of Maine: submersible experimentation and remote sensing. In: Babb I, DeLuca M (eds). Natl Undersea Res Prgm Res Rep 88–3, Rockville, MD pp. 143–176

Bigelow HB, Schroeder WC (1953) Fishes of the Gulf of Maine. U.S. Fish. Wild. Serv. Fishery Bulletin. 53

Breen PA, Mann KH (1976) Changing lobster abundance and the destruction of kelp beds by sea urchins. Mar Biol 34:137–142

Brown BE, Brennan JA, Grosslein MD, Heyerdahl EG, Hennemuth RC (1978) The effect of fishing on the marine finfish biomass in the northeast Atlantic from the Gulf of Maine to Cape Hatteras. ICNAF Res. Bull 12:49–69

Castilla JC, Duran R (1985) Human exploitation from the intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda) Oikos 45:391–399

Choat JH (1982) Fish feeding and the structure of benthic communities in temperate waters. Ann Rev Ecol Syst 13:423–449

Connell JH (1970) A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol Monogr 40:49–78

Connell JH (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities Harvard University Press, Cambridge pp 460–490

Cowen RK (1983) The effect of sheephead *(Semicossyphus pulcher)* predation on red sea urchin *(Stronglyocentrotus franciscanus)* populations: an experimental analysis. Oecologia 58:249–255

Dayton PK, Tegner MJ (1984) The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In: Price PW, Slobodchikoff CN, Gaud WS (eds) A new ecology: novel approaches to interactive systems Wiley & Sons, New York, pp. 457–481

Denman KL, Powell TM (1984) Effects of physical processes on planktonic ecosystems in the coastal ocean. Oceanogr. Mar Biol Ann Rev 22:125–168

Dethier MN, Duggins DO (1989) Variation in strong interactions in the intertidal zone along a geographical gradient: a Washington – Alaska comparison. Mar Ecol Prog Ser 50:97–105

Duggins DO (1980) Kelp beds and sea otters: an experimental approach. Ecology 61:447–453

Elner RW (1980) Predation on the sea urchin *(Stronglyocentrotus drobaciensis)* by the american lobster *(Homarus americanus)* and the rock crab *(Cancer irroratus)*. In: Pringle JD, Sharp GJ, Caddy JF (eds) Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal harvesting. Can Tech Rep Fish Aq Sci No 954 pp 48–65

Elner RW, Campbell A (1987) Natural diets of lobster *Homarus americanus* from barren ground and macroalgal habitats off southwestern Nova Scotia, Canada. Mar Ecol Prog Ser 37:131–140

Elner RW, Vadas RL (1990) Inference in ecology: the sea urchin phenomenon in the northwest Atlantic. Am Nat 136:108–105

Estes JA, Smith NS, Palmisano JF (1978) Sea otter predation and community organization in the western Aleutian Islands, Alaska. Ecology 59:822–833

Etter RJ (1989) Life history variation in the intertidal snail *Nucella lapillus* across a wave exposure gradient. Ecology 70:1857–1876

German AW (1987) History of the early fisheries: 1720–1930. In: Backus R H, Bourne DW (eds) Georges Bank. M.I.T. Press, Cambridge pp 409–424

Hacunda JS (1981) Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine. Fish Bull 79:745–788

Hay ME (1984) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? Ecology 65:446–454

Heck KL, Thoman TA (1981) Experiments on predator-prey interactions in vegetated aquatic habitats. J Exp Mar Biol Ecol 53:125–134

Heck KL, Wilson KA (1987) Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques J Exp Mar Biol Ecol 107:87–100

Hixon MA, Brostoff WN (1983) Damselfish as keystone species in reverse: intermediate disturbance and diversity of reef algae. Science 220:511–513

Hulbert AW, Pecci KJ, Witman JD, Harris LG, Sears JR, Cooper RC (1982) Ecosystem definition and community structure of the macrobenthos of the NEMP monitoring station at Pigeon Hill in the Gulf of Maine. Natl. Oceanic Atmos. Adm. Tech. Mem. NMFS–F/NEC–14 Woods Hole, MA

Huitema BE (1980) The analysis of covariance and alternatives. John Wiley & Sons, New York

Innis HA (1940) The cod fisheries. Yale Univ. Press, New Haven

Jensen AC (1972) The cod. Crowell Press, New York

Jonsson G (1982) Contribution to the biology of the catfish *(Anarhichas lupus)* Rit Fiskideildar 6:2–26

Keats DW, Steele DH, South GR (1986) Atlantic wolffish (*Anarhichas lupus* L. Pisces: Anarhichidae) predation on green sea urchins (*Strongylocentrotus droebachiensis* O.F. Mull.; Echinodermata: Echinoidea) in eastern Newfoundland. Can J Zool 64:1920–1925

Keats DW (1990) Food of winter flounder, *Pseudopleuronectes americanus* in a sea urchin dominated community in eastern Newfoundland. Mar Ecol Progr Ser 60:13–22

Langton RW (1982) Diet overlap between Atlantic cod, *Gadus morhua,* silver hake, *Merluccius bilinearis,* and fifteen other northwest Atlantic finfish. Fish Bull 80:745–759

Levin SA (1988) Sea otters and nearshore benthic communities: a theoretical perspective In: Van Blaricom GR, Estes JA (eds) The community ecology of sea otters. Springer-Verlag, Berlin pp 202–209

Menge B.A. (1976) Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Eco Monogr 46:355–393

Menge BA (1978) Predation intensity in a rocky intertidal community: effect of an algal canopy, wave action and desication on predator feeding rates. Oecologia 34:17–35

Menge BA, Sutherland JP (1976) Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am Nat 110:351–369

Menge BA, Lubchenco J (1981) Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. Ecol Monogr 51:429–540

Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am Nat 130:730–757

Menge BA (1978) Predation intensity in a rocky intertidal community: effect of an algal canopy, wave action and dessication on predator feeding rates. Oecologia 34:17–35

Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. Trends Ecol Evol 5:52–57

Miller TE, Kerfoot WC (1987) Redefining indirect effects. In: Kerfoot WC, Sih A. (eds) Predation: direct and indirect impacts on aquatic communities. Univ, Press of New England, Hanover, NH, pp. 33–37

Moran ML, Fairweather PG, Underwood AJ (1984) Growth and mortality of the predatory intertidal whelk *Morula marginalba;* the effects of different species of prey. J Exp Mar Biol Ecol 75:1–17

Moreno CA, Lunecke KN, Lopez MI (1986) The response of an intertidal *Concholepas concholepas* (Gastropoda: Muricidae) to protection from man in southern Chile and its effects on benthic sessile assemblages. Oikos 46:359–364

Ojeda FP (1987) Rocky subtidal community structure in the Gulf of Maine: the role of mobile predators Dissertation, University of Maine, Orono, ME. USA

Ojeda FP, Dearborn JH (1991) Feeding ecology of benthic mobile predators: experimental analyses of their influence in rocky subtidal communities of the Gulf of Maine. J Exp Mar Biol Ecol 149:13–44

Paine RT (1966) Food web complexity and species diversity. Am Nat 100:65–75

Paine RT (1976) Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. Ecology 57:858–873

Peterson CH (1982) Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density and seagrass cover. Mar Biol 66:159–170

Roughgarden JS, Gaines S, Possingham G (1988) Recruitment dynamics in complex life cycles. Science 241:1460–1466

Rich WH (1929) Fishing grounds of the Gulf of Maine. Bureau of Fisheries 1059:51–118

Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. Science 235:167–171

Sears JR, Cooper RA (1978) Descriptive ecology of offshore, deep water, benthic algae in the temperate western North Atlantic Ocean. Mar Biol 44:309–314

Sebens KP (1986) Community ecology of vertical walls in the Gulf of Maine, USA: small scale processes and alternative community states. In: Moore PG, Seed R (eds) The ecology of rocky coasts. Hodder and Stoughton, London pp 346–371

Sette OE (1928) Statistics of the catch of cod off the east coast of North America. U.S. Bureau of Fisheries, Report of the U.S. Commissioner of Fish and Fisheries for 1927 9:737–748

Simenstad CA, Estes JA, Kenyon KW (1978) Aleuts, sea otters, and alternate stable-state communities. Science 200:403–411

Summerson HC, Peterson CH (1984) Role of predation in organizing benthic communities of a temperate-zone seagrass bed. Mar Ecol Prog Ser 15:63–77

Thorson G (1957) Bottom communities In: Hedgepeth JW (ed) Treatise on marine ecology and paleoecology. Geol Soc Am Mem 67:461–534

Vadas RL, Elner RW, Garwood PE, Babb IG (1986) Experimental evaluation of aggregation behavior in the sea urchin *Strongylocentrotus droebachiensis*. Mar Biol 90:433–448

Vadas RL, Steneck RS (1988) Zonation of deep water benthic algae in the Gulf of Maine. J Phycol 24:338–346

Van Blaricom GR, Estes JA (1988) The community ecology of sea otters. Springer – Verlag, Berlin

Vermeij GJ (1976) Interoceanic differences in vulnerability of shelled prey to crab predation Nature 260:135–136

Vermeij GJ (1978) Biogeography and adaptation. Harvard University Press, Cambridge, MA

Wahle RA (1988) Recruitment and body size-dependent habitat selection and predator impact in early benthic phase american lobsters. Am Zool 28:5A

Wahle RA (1990) Recruitment, habitat selection, and the impact of predators on the early benthic phase of the American lobster *(Homarus americanus)* PhD dissertation, Univ. of Maine

Watanabe JM (1984) The influence of recruitment, competition, and benthic predation on the spatial distributions of three species of kelp forest gastropods (Trochidae: *Tegula*) Ecology 65:920–936

Witman JD (1985) Refuges, biological disturbance and subtidal community organization in New England Ecol Monogr 55:421–445

Witman JD, Cooper RA (1983) Disturbance and contrasting patterns of population structure in the brachiopod *Terebratulina septentrionalis* (Couthouy) from two subtidal habitats. J Exp Mar Bio Ecol 73:57–79

Witman JD, Sebens KP (1988) Benthic community structure at a subtidal rock pinnacle in the central Gulf of Maine. In: Babb I, DeLuca M (eds) Natl. Undersea Res. Prgm. Res. Rep. 88–3, Rockville, MD, pp 67–104

Witman JD, Sebens KP (1990) Distribution and ecology of sponges at a subtidal rock pinnacle in the central Gulf of Maine In: New Perspectives in Sponge Biology. Rutzler K (ed) Smithsonian Institution Press, Washington, D.C., pp 391–396

Wolanski E, Hamner WM (1988) Topographically controlled fronts in the ocean and their biological influence. Science 241:177–181

Woodin SA (1978) Refuges, biological disturbance, and community structure: a marine soft bottom example. Ecology 59:274–284

Zar JH (1981) Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ