The Marine Community in a Nearshore Rocky Habitat in Nova Scotia

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ABSTRACT

Miller, R.J., Davis, N.D., and Meade L.D. 2014. The marine community in a nearshore rocky habitat in Nova Scotia. Can. Tech. Rep. Fish. Aquat. Sci. 3104: 62 p.

The current fisheries habitat regulatory regime manages threats to the sustainability and productivity of specified types of fish habitat. Habitat baseline conditions are useful to identify changes. For a nearshore rocky bottom habitat we report on macrophyte biomass and depth distribution, benthic biomass divided into size classes and feeding types, epibenthic plankton biomass, fish abundance based on capture rate in nets, fish stomach contents, and trap catches of rock crab and American lobster. Observations were over 2-3 years in a sheltered bay on the outer coast of Nova Scotia.

Irish moss and kelp macrophytes dominated the habitat not affected by sea urchin grazing. In areas where sea urchins were manually removed or died from disease much of the habitat was subsequently colonized by *Fucus* and *Laminaria*. Rock crabs were larger and catches higher in kelp than on macrophyte free bottom. Lobster catches did not differ between the edges of macrophyte and macrophyte-free habitats. Cunner and rock gunnel dominated fish larval collections in epibenthic plankton. Biomass (ash free dry weight) in epibenthic plankton was 56% omnivores/detritovores (O/D) and 29% grazers. Biomass of benthos was greater on the shallow than deep ends of transects. Benthic predator and O/D biomass was usually higher than suspension feeder and grazer biomass. Benthic biomass decreased with animal sizes from <2 mm to 2-4 mm to 4-8 mm, but increased for 9-16 and >16 mm categories. Larger sizes were dominated by mussels, periwinkles, and *Cancer* crabs. Few spatial correlations of macrophyte biomass with size or feeding type of benthic biomass were significant. O/D was positively correlated with small macrophytes and grazers negatively correlated with kelp. The most abundant fish species caught in trammel nets were pollock, cod, and cunner. Pollock recruited to the area at ~4 cm length and increased in weight by more than an order of magnitude from July to December. Cod were caught over a wide range of sizes with no clear cohorts. There were also no clear spatial relationships of fish catches to macrophyte biomass. Stomach contents of small pollock were dominated by copepods with shrimp and fish more important for larger pollock. *Cancer* crabs were an important diet component for larger cod, with fish, shrimp and mysids eaten by all cod sizes. Using production/biomass ratios from the literature, annual production was estimated for macrophytes and for size intervals and feeding types of benthos. Averaged over 3-years, in units of g ash free dry weight per m^2, production was 840 for macrophytes, 13 for grazers, 2 for O/D, 6 for suspension feeders, and 2 for predators. The total production for epibenthic plankton of all feeding types was small at 0.1 g ash free dry weight per m^2.

RÉSUMÉ

Miller, R.J., Davis, S.D., and Meade, L.D. 2014. La communauté d’organismes marins dans un habitat rocheux situé près des côtes de la Nouvelle-Écosse. Can. Tech. Rep. Fish. Aquat. Sci. 3104: 62 p.

L'actuel régime de réglementation des habitats qui soutiennent les pêches permet de gérer les menaces qui pèsent sur la durabilité et la productivité de types précis d'habitat du poisson. L'état de référence de l'habitat contribue à déterminer les changements. Le présent rapport porte sur la biomasse des macrophytes et leur répartition selon la profondeur, la biomasse benthique divisée en catégories de tailles et de types d'alimentation, la biomasse du plancton épibenthique, l'abondance du poisson en fonction des taux de capture dans les filets, les contenus stomacaux de poissons et les prises dans les casiers de crabes communs et de homards dans un habitat rocheux côtier. Les observations ont été effectuées sur une période de deux à trois ans dans une baie abritée sur le littoral extérieur de la Nouvelle-Écosse.

Les macrophytes, comme la mousse d'Irlande et le varech, dominaient l'habitat qui n'était pas touché par le broutage par les oursins. Dans les zones où les oursins étaient retirés à la main ou dans lesquelles ils mourraient de maladie, la majeure partie de l'habitat était par la suite colonisée par les algues *Fucus* et *Laminaria*. Les crabes communs étaient plus gros et les prises plus importantes dans le varech que sur les fonds sans macrophytes. En ce qui concerne les prises de homards, il n'y avait aucune différence selon qu'elles avaient été effectuées au bord d'habitats constitués de macrophytes ou d'habitats sans macrophytes. La tanche-tautogue et la sigouine de roche étaient les plus nombreuses dans les collectes de larves de poisson effectuées dans le plancton épibenthique. La biomasse (poids sec sans cendre) dans le plancton épibenthique comprenait 56 % d'omnivores et de détritivores (O/D) et 29 % de brouteurs. La biomasse de benthos était plus importante dans les eaux peu profondes que dans les extrémités des transects où l'eau est plus profonde. La biomasse des prédateurs benthiques et des O/D était généralement plus élevée que la biomasse des organismes suspensivores et des brouteurs. La biomasse benthique diminuait pour les animaux dont la taille était < 2 mm jusqu'à 2-4 mm et 4 à 8 mm, mais elle augmentait pour les catégories 9 à 16 mm et > 16 mm. Les plus grandes tailles étaient dominées par les moules, les bigorneaux et les crabes *Cancer*. Peu de corrélations spatiales significatives de la biomasse des macrophytes avec la taille ou le type d'alimentation de la biomasse benthique ont été observées. Les O/D étaient en corrélation positive avec les petites macrophytes, et les brouteurs étaient en corrélation négative avec le varech. Les espèces de poissons les plus abondantes capturées dans les trémails étaient la goberge, la morue et la tanche-tautogue. Les goberges recrutées dans la zone étaient d'environ 4 cm de longueur et ont augmenté leur poids par plus d'un ordre de grandeur de juillet à décembre. Les morues qui ont été capturées appartenaient à une vaste gamme de tailles sans distinction nette entre les cohortes. Il n'y avait également pas de relations spatiales claires entre les prises de poisson et la biomasse de macrophytes. Les contenus stomacaux des goberges de petite taille comprenaient principalement des copépodes, tandis que ceux des goberges de plus grande taille comprenaient des quantités plus importantes de crevettes et de poissons. Les crabes *Cancer* constituaient une importante composante du régime alimentaire des morues des plus grandes tailles, tandis que les morues de toutes les tailles se nourrissaient de poissons, de crevettes et de mysidacés. À l'aide des rapports production/biomasse tirés de la littérature, on a estimé la production annuelle des macrophytes ainsi que les intervalles entre les tailles et les types d'alimentation des benthos. La moyenne sur trois ans de la production, en grammes de poids sec sans cendre par mètre carré, a été de 840 pour les macrophytes, de 13 pour les brouteurs, de 2 pour les O/D, de 6 pour les organismes suspensivores et de 2 pour les prédateurs. La production totale de plancton épibenthique de tous les types d'alimentation a été faible, se montant à 0,1 g de poids sec sans cendre par mètre carré.

INTRODUCTION

Here we describe inshore marine habitats and biota in a sheltered cove on the outer (Atlantic) Nova Scotia shore (Fig. 1). The physical habitat appeared to be unaltered by human activity, i.e. without dredging, infill, or a conspicuous source of pollution. The bottom type and exposure to waves in the study area represents 259 km of the 2894 km of total shoreline length and the 1400 km of the shoreline bordered by rocky bottom (Miller 1985a) on the eastern end and outer coast of Nova Scotia. If we include the three most sheltered of five wave exposure categories, then represented shoreline length increases to 657 km. Rocky bottom continued to greater depth with more wave exposure, but otherwise the habitat and macrophytes were not greatly different from the study area (Moore and Miller 1983; Moore et.al. 1986).

Inshore macrophytes have been described in detail for the outer coast of Nova Scotia (Edelstein et al. 1969; Mann 1971; Breen and Mann 1976; Chapman 1981; Miller 1985a) as have sea urchins (Mann 1977; Chapman 1981; Wharton and Mann 1981; Moore et. al. 1986; Balch and Scheibling 2000, and several others). Observations of biomass and size distributions of American lobster (*Homarus americanus*) and rock crab (*Cancer irroratus*) were reviewed in Miller (1985b; 1995). Most studies of shallow water invertebrates on this shore have been on soft bottom fauna, but studies of hard bottom fauna include macrophyte epifauna (Schmidt and Scheibling 2006; Saunders and Metaxis 2007), grazing and predator gastropods (Johnson and Mann 1986; Hunt and Scheibling 1998), green crab (*Carcinus maenas*) (Elner 1981), and sea stars (Scheibling and Lauzon-Guay 2007).

The initial intent of the study was to compare subtidal benthic community structure in three treatments related to macrophyte cover: a dense bed of mature kelp (*Laminaria sp.)* and Irish moss (*Chondrus crispus)*, a developing macrophyte bed following removal of grazing sea urchins, and a control where sea urchins remained. However, this objective was thwarted by mass mortality of sea urchins from disease (Miller 1985a) in the control area a few months after they were manually destroyed in the removal area. We continued with a study of the flora and fauna to describe community structure.

A 2012 Government of Canada policy (Bill 38) directs the Fisheries Act regulatory regime to manage threats to the sustainability and ongoing productivity of Canada's commercial, recreational and Aboriginal fisheries and the permanent alternation or destruction of fish habitat. Here we provide results of 2-3 years of sampling macrophytes, benthic invertebrates, epibenthic plankton, fish, and fish stomach contents. Correlations of animal and plant biomass were investigated. We recommend results of this study as a proxy for “before disturbance” conditions of fish habitat. Estimates of annual production, fish feeding, and biomass by size class may also be useful for modeling ecosystem function.

METHODS

STUDY AREA

This study was located in a shallow and sheltered, subtidal area between the villages of McGrath Cove and East Dover 24 km southwest of Halifax at 44.30^{o}N by 63.51^{o}W (Fig. 1). There was no line of sight to the open sea and the longest open-water fetch was 2 km to the southeast. The largest waves round a headland to the southeast and could reach 1.5 m high; but were usually less than 0.5 m. The area extended 200 m along shore and 20-60 m from shore. Tidal range was 0.9-1.5 m. Current speeds were low but not measured. The location was chosen for ease of access by small boats, cooperative fishermen, and a mature kelp bed adjacent to a barren area grazed free of macrophytes by sea urchins.

Salinity was not measured, but freshwater runoff was from only small seasonal streams. Salinity nearshore in this area is near 30 o/oo year-around (pers. comm., A. Moore, Bedford Inst. of Oceanography) with lower salinity in a shallow surface layer during periods of heavy runoff. Temperature records are presented later.

The substrate from high tide to about 2 m below mlw was granite bedrock. Granite boulders and cobble dominated from 2 to 5-9 m depth, then changed abruptly to silt covered gravel with only a slight slope.

The narrow intertidal zone had near 100% cover of rock weed (*Ascophyllum nodosum*) in all treatments. Sampling began below the rockweed. Numbered signs were placed every 10 m along shore as aids for choosing sampling locations.

The kelp treatment was located on the east side of the area and delineated by signs 1-4. This treatment was dominated by a boulder ridge. Dense cover of Irish moss (*Chondrus crispus*) extended from mlw to about 2 m depth, then a mature kelp bed (*Laminaria longicruris*) with plants up to 3 m long and 0.7 m wide covered the remainder out to 9 m depth and 60 m from shore.

The removal treatment was marked by signs 5-11 and extended 20-30 m from mlw to 7-8 m depth. It was kept mostly free of macrophytes by green sea urchin (*Strongylocentrotus droebachiensis*) grazing until we intervened. In December 1980 about one-half of the urchins were killed by spreading quicklime from the surface. In May 1981 divers completed urchin removal by breaking their tests with hammers.

The control treatment to the west was marked by signs 12-19 and extended 20-60 m from mlw to 5-8 m depth. This area was also kept mostly free of macrophytes by sea urchin grazing. We did not remove the urchins here. A 1 m high net fence placed at the border of the control and removal areas prevented urchins from re-invading the removal treatment.

SAMPLING

Seven types of samples were taken in each of the three treatment areas: (1) epibenthic plankton <8 mm using a plankton net, (2) animal benthos <8 mm and small macrophytes using diver operated suction sampling of 0.065 m^2 quadrats, (3) animal benthos >8 mm and kelp by a diver hand picking 0.4 m^2 quadrats, (4) stationary trammel nets to catch fish, (5) stomach analyses of fish caught in trammel nets, (6) crab traps for crabs, and (7) lobster traps for lobsters. On a few occasions a beach seine was also fished along shore to catch smaller fish than were captured in trammel nets. Epibenthic plankton was sampled over silt just below the control area in addition to the three treatment areas, and crab and lobster traps were fished in additional nearby paired kelp-barren areas. The numbers of collections by date are listed in Table 1. In most cases sampling was carried out on multiple dates to achieve the desired number of replications to represent a sampling period. See the Appendix for photos of the habitat and sampling gear.

Crab and lobster trapping

Crab trapping compared the catch rates of *Cancer* crabs (about 90% *C. irroratus* and 10% *C. borealis*) between the three experimental areas as well as between two paired areas of dense kelp and urchin dominated barrens. The paired areas were within a few km of the experimental areas and of similar depth and bottom type. The paired areas allowed us to fish more traps without their competing for catch in the small experimental areas. All traps were set in August-October, 1981 at depths between 4 and 8 m on rocky bottom. They were set deeper than 4 m to avoid the abundant green crabs (*Carcinus maenas*). Traps were cone shaped with 70 cm bottom diameter, 30 cm top diameter, by 30 cm high and constructed of metal rod covered with 3 cm stretch nylon mesh. A 20 cm circular top entrance was fitted with a recessed plastic cone to prevent crabs from escaping. Traps were baited with about 300 g of frozen Atlantic mackerel hanging from the entrance cone. There were a total of 130 trap hauls. Lobster traps were set at the same sites, except they were set on the mud at the interface of rock and mud bottom. This location was chosen on the advice of local lobster fishermen who claimed the best catches were made at the deep edge of kelp beds. Traps were positioned by divers and spaced 10 m apart. The wooden-framed parlour traps, about 90 by 50 by 40 cm high were covered with wooden lath spaced 1 cm apart. The side entrance rings were only 7.5 cm diameter to exclude most commercial sized lobsters (Stasko 1975), and reduce bias in catches caused by removals by the fishery. Most of the annual molting would have occurred between the end of the fishing season in May and our trap fishing, thus replenishing the 8.1-9.3 cm carapace length (CL) molt class just over minimum legal size. Bait was about 300 g of Atlantic mackerel placed on a spike in the center of the trap. There were 114 trap hauls.

Epibenthic plankton sampling

Each net tow represented a sample area of 40 m^2 and sample volume of 25 m^3. A 1 mm mesh net with a rectangular mouth opening 65 cm wide by 37 cm high was towed at about 1 m/sec for about 61 m. Distances were initially measured using a calibrated flow meter in the net. An outboard powered skiff towed a diver holding onto the sides of the net frame steering it just over the bottom or through macrophytes. Sample frequency was usually two tows per treatment per day and 2-days per time period. Tows were diagonal shallow to deep and deep to shallow alternating between east to west and west to east. Tow depths were typically 2-8 m, 1-6 m and 1-7 m below mlw in kelp, removal, and control treatments respectively. A silt treatment was 8-9 m deep in a 20 by 60 m area below the control treatment. After each tow the net was taken to the skiff where the catch was preserved in 4% buffered formalin.

In the laboratory catches were divided into 12 categories: feeding types of suspension, predator, grazer, and omnivore/detritovores (O/D) and sizes of <2, 2-8, and >8 mm. The largest size category was discarded because mobile animals would likely escape the net and sessile ones, mostly snails, would be included in benthic samples. The size measurement was of the second largest dimension, i.e. the diameter of a cylinder that the specimen could pass through. Examples are the length of a crab, or height of a fish. For each category blotted wet weight, dry weight after drying overnight at 60^{o}C, and ash-free-dry-weight (AFDW) after ashing at 450^{o}C for 90 min were measured. Ninety minutes was chosen because dry weight decreased and AFDW (by subtraction) increased 18% from 30 to 90 min but only 1.5% from 90 to 120 min. The ashing temperature was chosen to be high enough to ash the organic matter but not so high as to drive off the bound water in calcium compounds. Only AFDW measurements will be reported. Species of juvenile/larval fish were consistently identified from only the first four of 10 sampling periods.

Trammel nets and seine

Trammel nets were chosen to provide relative abundances of fish species, fish sizes, and samples for stomach contents. Our nets had two outside mesh walls of 30 x 30 cm and a slack small mesh wall of 2.5x2.5 cm between the two large meshes. The smallest fish caught would gill themselves in the small mesh and larger fish would swim through the near large mesh, push a pocket of small mesh netting through the far large mesh, and/or simply tangle themselves in the small mesh. Pollock (*Pollachius virens*)as short as 9 cm and flatfish as short as 8 cm were captured. Cod (*Gadus morhua*) up to 65 cm and skate with a wing width of 50 cm were captured. Nets were 1.8 m by 20 m. They were set on bottom and held vertical by buoyant top rope.

Each net was set perpendicular to shore off a randomly selected 10 m mark in each of kelp, removal, and control treatment areas with the shallow end just below the *Ascophyllum* zone. Soak time was 2.0-

2.4 h centered on dusk. Catch was removed from the nets and placed in a cooler on ice and transported to the laboratory. There, fish were measured to 1 mm fork length, guts removed, labeled, and preserved in buffered formalin and sea water within 4-5 h of fishing. For each sampling period this procedure was repeated on 4-days for a total of 12 net hauls.

To measure diurnal variation, during September 10-11, 1981 three nets were fished five times in 24 h. Fishing and removal of guts was as above except the randomly selected locations were only in control and removal areas.

A seine was hauled near shore in the kelp treatment on three dates to capture fish smaller than retained by trammel nets. The seine was 1.8 m x 45 m long with 4.8 x 6.3 mm oval mesh. One end was held at the water's edge while the other was stretched full length perpendicular to shore then towed into shore by a small outboard skiff sweeping an arc of 10-40 m radius. A diver followed the net into shore releasing the foot rope from bottom obstructions. The swept area was not consistent. Only pollock were recorded; 5% was added to their lengths to account for shrinkage in formalin.

Fish stomach contents

Total blotted weight of stomach contents was measured to the nearest mg in both 1981 and 1982. In 1981 an estimated percentage of each taxon (e.g. copepods, *Gammarus, Lacuna*, *Skeneopsis*) was recorded. In 1982 the blotted wet weight of each feeding type was measured and principal taxa noted.

Epibenthic plants and animals less than and greater than 8 mm

One of the 10 m marks on shore in each treatment area was chosen from a random numbers' table. Below the 10 m mark a diver laid a sinking transect line perpendicular to shore starting below the *Ascophyllum* zone and ending where the silt bottom began. From this line, marked at 1-m intervals, the diver noted the number of meter marks located in the shallow and deep halves of the transect, omitting the top and bottom marks to reduce contamination by fauna from the *Ascophyllum* and silt habitats. He gave this information to the boat attendant, who in turn gave the diver two randomly selected meter marks in each half.

For collection of fauna <8mm and sea weeds other than kelp, the diver placed a 0.065 m^2 quadrat at the bottom left of a meter mark. The quadrat represented a horizontal plane and all surfaces under this projected area were sampled, including under the top layer of cobbles when they were present. The substrate was scraped clean with a paint scraper and vacuumed with a 1-m long air-lift sampler powered from the divers SCUBA tank. A 1 mm mesh sock with a removable plastic bottle was attached to the top of the sampler. The diver vacuumed two quadrats from the shallow end into the same sample. The boat attendant emptied the sample onto a 1 mm mesh sieve then discarded inanimate material and animals >8mm (in the second largest dimension) and preserved the sample in 10% buffered formalin and sea water. This was repeated for the two deep quadrats and the line moved to another randomly selected 10 m mark.

For fauna >8mm and kelp the diver placed a 3-sided 0.4 m^2 quadrat at the top right of a meter mark. Here the diver gathered animals and kelp by hand and placed them in a mesh bag, combining samples from two quadrats as before. A boat attendant transferred samples into numbered mesh bags.

In the laboratory animals <8 mm from the small quadrats were sorted into <2, 2-4 and 4-8 mm size classes and the same feeding types as for epibenthic plankton. For each size and feeding category animal were dried overnight at 65^{o}C and ashed for 90 min at 450^{o}C to obtain AFDW. Small plants were blotted and weighed wet. Plant weight/m^2 was obtained by summing weight/m^2 from small and large quadrats.

In the laboratory the unpreserved samples from the large quadrats were sorted the same day as collected. Animals were separated into 8-16 and >16 mm size classes and into feeding types of suspension, predator, grazer, and O/D. Each category was weighed wet; mussels were drained before weighing. AFDW was obtained using conversion factors from smaller animals of the same species. Kelp was weighed damp. Animals <8mm from the large quadrats were discarded. To dry and ash large animals would have added greatly to the cost of sample processing, requiring long drying times and more oven space.

The above procedure was repeated three times for each of five sampling periods from June 1981 to June 1983, with the exception of one transect missing in the control treatment in August 1981 and the shallow portion of one transect in the kelp treatment on the same date. Thus, 174 large (4 quadrats per transect, 3 treatments, 3 days per sampling period, 5 sampling periods) and 174 small quadrats were sampled with collections from two quadrats combined for each sample.

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RESULTS

CRAB AND LOBSTER TRAPPING

Traps were fished 2-days in paired barren-kelp areas A-B and 3-days in paired barren-kelp areas C-D. Control, removal, and kelp experimental treatments were also fished. New kelp had begun to grow in the removal area and was about 0.5 m long. Although trap soak times varied between days, fishing times were the same within days for comparisons between habitats. The maximum size of crabs caught was 12 cm carapace width (CW) and the minimum size included in the analysis was 6.5 cm CW. All lobster sizes captured were included in the analysis and ranged from 4.6-9.2 cm carapace length (CL).

Using chi-square analysis, total crab catch in a barrens area was compared to total catch in a kelp area (Table 2). The "expected" catch was assumed to be the average of the catch across treatments (e.g. the mean of 6 and 22 in the first entry of Table 2). For both A vs. B and C vs. D area comparisons catch rates were significantly higher in kelp. Overall means were 1.0 (areas A and C) and 4.9 (areas B and D) crabs/trap for barrens and kelp respectively. For the experimental areas means were 2.0, 2.9, and 5.7 crabs/trap for control, removal, and kelp respectively. Catches in the kelp treatment were significantly higher than in the other two. New kelp had begun to grow in the removal area and was about 0.5 m long.

Using one-way ANOVA, mean crab sizes were also compared among treatments (Table 2). Crabs were significantly larger in kelp for areas A vs. B and C vs. D. For the experimental treatments crabs were significantly larger in kelp than in the control site. Size was numerically intermediate in the removal treatment but was not significantly different from the other two.

Lobster catches were compared the same way for the same areas (Table 2). There were no differences between catch rates for any of the areas. Overall means for areas A and C and B and D were 1.8 and 2.2 lobster/trap haul for barrens and kelp respectively. For the experimental treatments means were 2.3, 2.3, and 1.9 lobsters/trap haul for control, removal, and kelp respectively. Thus the claim of lobster fishermen that the deep edges of kelp beds give the best catches was not supported.

Lobster sizes did not differ between kelp and barrens for areas A vs. B and C vs. D, but were significantly smaller in the control than the other two experimental areas.

Both Cancer crabs and lobsters were well represented in the fauna.

EPIBENTHIC PLANKTON
Counts of fish larvae and small juveniles by species were available from June-Oct., 1981; but were not always counted in subsequent samples. Only results for fish <8 mm are presented because the larger fish were more likely to avoid the net.

By far the most abundant fish captured in the plankton samples were rock gunnel (*Pholis gunnellus*) and cunner (*Tautogolabrus adspersus*). Gunnel dominated in June and July and cunner in August, 1981 (Fig. 2). Both species were always rare over silt bottom and (by inspection) both were most abundant in the removal treatment.

Other species were present in much lower abundance. Their total number in 72 samples were: short-horn sculpin (*Myoxocephalus scorpius*) - 12, grubby (*Myoxocephalus aenreus*) -13, winter flounder (*Pseudopleuronectes americanus*) -5, lumpfish (*Cyclopterus lumpus*) -12, cod (*Gadus morhua*) -1, pollock (*Pollachius virens*) -1, and white hake (*Urophycis tenuis*) -1. In 1982 samples pollock were noted (but not counted) in three samples in early June and winter flounder on five occasions in August. Thus, small individuals of commercial species were uncommon during the June-October sampling.

Table 3 summarizes survey results for abundant taxa (means of four 40 m^2 samples) by date and Fig. 3 summarizes by mg AFDW. The towed net knocked animals off the seaweeds but did not scrape them from the bottom. Over all habitats and dates suspension feeders, predators, grazers, and O/D were 2%, 13%, 29%, and 56% respectively of total AFDW. Highest total biomass was in kelp and removal areas and the lowest in control and silt areas. By inspection, O/D was the dominant feeding type over silt for all dates with a peak in autumn. Shrimp, *Eualis* and *Crangon*, and mysids dominated. In the mature kelp bed O/D again dominated over all seasons with mysids, gammarids, and shrimp the most important. Nereid polychaetes and blood stars were often present with lower biomass. Grazers were always a small portion of biomass in kelp beds. Gunnel and other small fish were the dominant predators in kelp with Stauromedusae frequently present. Grazers were abundant in removal and control areas with *Lacuna* nearly always the most important species. O/D, comprising mysids, shrimp, and gammarids, made a significant contribution to biomass in removal and control areas. Small fish were the dominant predators. Suspension feeders were rare off bottom, but were mostly mussels when present.

Plankton and macroalgal biomass per m^2 were not well correlated. Algal-plankton correlations for the three hard-bottom treatments and five sampling periods in common for1981 and 1982 (n=15) for macrophytes vs. suspension feeders, vs. grazers, vs. predators, and vs. O/D were r= -0.15, -0.09, 0.54, and 0.57 respectively. Correlations for predator and O/D biomass were significant at $P<0.05$. We would not expect a correlation with suspension feeders as they were rare in the plankton. The lack of correlation with grazers was unexpected. Perhaps they were not well sampled, or grazing on the rock substrate was as beneficial as grazing on large macrophytes.

TRAMMEL NETS AND SEINE
In September, 1981 trammel nets were fished five times in 24 h to infer the relationship between fish catches at sunset, the time chosen for surveys, and other times of day. The four most abundant species in the catch are shown in Fig. 4. Catches at 1500h and 0030 h were low for all four species, and at 1030h low for three of the four. When all four species were combined (figure not included) mean catches per net haul were 3, 30, 7, 31, and 7 for times of 1500, 1930, 0030, 0530, and 1030 h respectively. Chi-square tests indicated the three low catches were different from the two high catches. Thus, if sunset was not the time of highest catch, it was near the highest.
Comparing *ln-ln* regressions of gut contents (mg wet weight) vs. fish length for each of the five haul times showed no trend. All fish species were combined in the regression, except for silver hake because

their guts were consistently empty. The change in species and fish sizes between times may account for the lack of trend.

For each of nine sampling periods in 1981-82 the total number of fish in four net hauls was compared among kelp, removal, and control treatments using 2-way ANOVA (treatment and haul). No significant difference was found between treatments ($P > 0.10$) for any of the nine dates. For five of the nine periods, when the number of fish caught were high enough for analysis, catches per treatment were compared after separating fish into groups of <20 cm and >20 cm total length. Again, no significant difference was found for these comparisons. Therefore, for the following comparisons between sampling periods, the catch in 12 net hauls representing three treatments and four hauls in each were combined.

Pollock, cod, and cunner were the most abundant of the 23 species captured by trammel nets (Table 4).

In Fig. 5 we can see the size modes of pollock advance through the seasons. In June 1981 a few fish formed a mode at 19-24 cm. By early July the mode had shifted to 21-28 cm and a new one appeared at 7-12 cm. In late August the number of small fish increased and had shifted to 11-14 cm. The mode of larger fish nearly disappeared. In October and December the small fish still comprised a large cohort and grew to 15-20 cm. The mode of large fish reappeared at 29-32 cm.

The smallest pollock in April 1982 were 15-20 cm compared to 19-24 cm in June 1981. The mode did not move in May, but increased to 18-20 cm in June, and to 21-28 in August. The new mode at 11-14 cm in August, 1982 was the same size as in August 1981.

A beach seine fished near the kelp treatment area in June and July 1981 and in June 1982 captured large numbers of pollock too small to be captured by the trammel nets. The June samples had modes at 4 and 5 cm and the July sample mode was 6 cm (Fig. 6). Thus, pollock at least as small as 4 cm were abundant in this habitat. The difference in modes for the two gears for the same dates is no doubt due to gear selectivity. The smaller fish were captured by the smaller mesh in the seine and the larger fish escaped the moving seine. However, because there was a mode at 6 cm we presume the 4 and 5 cm fish were not escaping capture. Cohorts are apparent from a plot of the means of the sizes in the modes from both gear types (Fig. 7).

If modes from seine and trammel nets represent pollock cohorts then growth is quite rapid. Based on these dates a live weight (g) to total length (cm) regression is

$$W = 0.0092\ L^{3.018} \qquad (n=52,\ 10\text{-}36\ \text{cm})$$

For the smaller cohort growth from ~5 cm in June to ~17 cm in December is indicated in Fig. 7. This gives a weight increase from 1.2 to 48 g. For the larger cohort, a pollock that is 18 cm in April-May and 31 cm in December increases from 57 to 292 g.

Although abundant, the progression of cod sizes is far less tidy with no clear cohorts (Fig. 5). In 1981 sizes from 11-12 to >47 cm were present in most samples June-December. In 1982 cod were scarce in April but again occurred over a large size range from May until the end of sampling in August.

Silver hake appeared from August to December in 1981, and in August, 1982, the last sampling date for that year (Fig. 8). They appeared to be all of one size cohort, 33-42 cm.

Cunner was abundant from June-October, but absent in early and late season (Fig. 8). Lengths were mostly 9-12 cm with a scattering among larger sizes.

Cunner presence-absence showed the most conspicuous relationship with temperature. They were first absent in early December 1981 when the temperature at all of 0, 4, and 8 m depth was 8^{o}C (Fig. 9). They were also absent in early April with temperatures at -1 to 5^{o}C and early May at 3-8^{o}C, but abundant in early June at 6-15 ^{o}C. Pollock were present on all dates from -1 to 19 ^{o}C and cod were present on all dates with no correlation with temperature (r= 0.13). Silver hake was present in only late summer and autumn, but without obvious correlation with temperature.

Winter flounder (not graphed) were present April-October and absent only in December.

Herring were poorly represented with only 3 Atlantic and 9 blueback. Although these are pelagic species one would expect catches in these shallow waters if abundant.

At least four common species were underrepresented in trammel net and benthos samples because of sampling selectivity. Grubby, rock gunnel (*Pholus gunnellus*) and radiated shanny (*Ulvaria subbifurcata)* were too small to be captured in trammel nets and too quick to be captured by quadrat sampling. Wrymouth (*Cryptacanthodes maculatus*) was present in burrows in the silt bottom but were not captured in nets set only on hard bottom.

Although total fish catch per 12 net hauls per sampling period was never low, 81 fish in May 1982 to 445 fish in August 1982, trammel net catch is not a sensitive estimate of abundance because catch in a stationary gear increases with fish activity. Schooling behaviour of silver hake and small pollock contributes greatly to the variance in capture rate.

SEAWEEDS

A prominent feature of sea weed biomass was the very high variability among samples taken at the same time in the same treatment (Fig. 10). This included differences between shallow and deep ends of transects and between randomly selected transects at similar depths in the same treatment. This variation occurred in spite of pooling two randomly selected quadrats in each sample. A five-fold range was not uncommon.

An increase in seaweed biomass (wet weight) in the removal and control treatments was not seen until the sample taken in late April 1982 (Fig. 10) even though the sea urchin die-off occurred in September 1981 and, sea urchins were destroyed in the removal treatment in May-June 1981. The control treatment did not develop a large kelp biomass but did develop stands of *Fucus* and *Chondrus*. The removal area developed a dense stand of small kelp by April 1982. Biomass increased to about 5 kg/m^2 at the deep half of transects in 1983 and 1984. The shallow biomass was dominated by 1-2 kg/m^2 of *Fucus, Chondrus,* and *Cystoclonium* through all of 1982-84.

The kelp treatment area was dominated by *Laminaria* in the deep portion and by *Chondrus* in the shallow portion (Table 5) throughout the study.

SEA URCHINS

June-81 samples were taken during the time urchins were being destroyed, but before the first appearance of disease in September 1981. By November-81 nearly all urchins were gone from all areas (Fig. 11). This condition remained through the two 1982 samplings. By June-83 small urchins were present in all three areas. Disease induced mortality probably recurred in the Autumn of 1983 because only very small urchins were present in June-84. Sea urchin biomass would have been too low to impact macrophyte growth after August-81.

ANIMAL BENTHOS < 8 MM

A sample was taken from the shallow and from the deep half of three transects in each treatment during each of six sampling periods. Variance among replications within sampling periods could be very large indicating large differences on a small spatial scale. A range of two orders of magnitude was not unusual (Fig. 12). There were no conspicuous seasonal trends for any of the feeding types (Fig. 12).

Two-way ANOVA and Tukey's W were used to compare AFDW/m^2 between four feeding types and between shallow and deep within each treatment (Table 6). Weights in all sizes <8 mm were summed. Data for all dates were included as replications in the analysis. In all three treatments the depth x feeding type interaction was insignificant, but the shallow biomass was greater than the deep ($P<0.01$). In the control treatment the biomass of the feeding types did not differ ($P=0.10$). In the removal treatment biomass of suspension feeders was significantly less than the other three feeding types ($P<0.01$). In the kelp treatment suspension and grazer biomass was similar, but both less than the similar predator and O/D biomass ($P<0.01$).

The high AFDW for suspension feeders in shallow water represent new settlement of blue mussels (*Mytilus edulis*) and occurred in the summer of all 3-years. Sponges were responsible for the single high value for suspension feeders in the deep half of the kelp treatment. Other prominent suspension feeders were a clam (*Hiatella artica)*, cockle (*Cerastoderma pinnulatum*), sessile tunicates, and brittle stars.

We captured many predator species including scale worms (*Harmothoe* sp.), other polychaetes, sea stars (*Astarias* sp.), *Cancer* crabs, dog whelk (*Nassarius trivitattus*), whelk (*Neptunea decemcostata*), nudibranchs, caprellid amphipods, stalked jellyfish (stauromedusae), pycnogonids, and juvenile fish. Scale worms and caprellids were probably the most numerous whereas sea stars, scale worms, and dog whelks probably represented the most AFDW. Although major species were recorded for each classification, counts of each were often not recorded.

The highest grazer AFDW for all years was in the shallow ends of all treatments and was predominately the small snail *Lacuna vincta*. Other snails (*Margarites sp*., *Skeneopsis planorbis*, *Littorina saxatilis*), slipper shells (*Crepidula fornicata*), and limpets (*Acmaea testudinalis*), were also prominent. The green sea urchin was sometimes abundant.

Among the O/D, amphipods (not identified) contributed the most to number, and amphipods and hermit crabs (*Pagurus* sp.) the most to biomass. Other prominent members of this large group were gastropods (*Hydrobia minuta*, *Cingula* sp.), bivalves (*Nuculana sp.*, *Tellina* sp.), shrimp (*Eualus* sp.), 10 familys of polychaetes (mostly *Nereis virens*), and spider crabs (*Hyas coarctatus*).

A complete list of species captured in benthic samples and their feeding type is found in Moore et al. (1982).

ANIMAL BENTHOS >8 MM

The larger benthic fauna included many fewer species than the <8 mm group. The AFDW of suspension feeders was dominated by the mussel *Mytilus edulus,* with horse mussels (*Modiolus modiolus)* and brittle stars (*Ophiopholis aculeata*) also abundant. In decreasing abundance, predators included *Cancer irroratus*, *Asterias* sp., *Cancer borealis*, and *Carcinus maenas*. Abundant grazers were *Littorina littorea* and *L. saxatalis,* with the green sea urchin prominent in June and August 1981, and June 1984. Few O/D reached >8 mm but two species of hermit crabs (*Pagurus acadianus* and *Pagurus arctuatus*) were the most common. O/D is not included in Fig. 13 because of low AFDW. Temporal and spatial variability was even higher for the large than for the small benthos (Fig. 13).

T-tests compared shallow to deep AFDW after transforming data as $\log_{10}$ (X+10 mg). Suspension feeders, predators, and grazers were all more abundant in shallow than deep halves of removal area transects. Grazers were most abundant in the shallow half of control transects and suspension feeders most abundant in shallow half of kelp transects.

BENTHIC BIOMASS BY FEEDING TYPE

Fig. 14 is a higher level summary than Figs. 12 and 13, summing all sizes <16 mm averaged over all three sampling treatments. Because the biomass >16 mm was usually greater than all other sizes combined it would mask trends if it was included in this summary. As noted in an above section, the >16 mm size interval included mostly, *Littorina*, *Mytilus*, and *Cancer*. Suspension, O/D, and predator had similar biomasses in the <16 mm category. The higher biomass for grazers was due to *Littorina* in the 9-16 mm category, plus sea urchin biomass for the first two sampling dates. Overall, AFDW means, including >16 mm, were 6.6, 14.0, 1.2, and 2.6 g AFDW/m^2 for suspension, grazers, predators, and O/D respectively.

BENTHIC BIOMASS BY SIZE CATEGORY

Fig. 15 identifies sizes and is also a higher level summary of Figs. 12 and 13. Among dates, on average, there is a decreasing biomass from sizes <2 to 4-8 mm. As noted, the higher biomass at 8-16 mm is mostly *Littorina* with the addition of sea urchins in the first two samples, and the ≥16 mm category was not plotted because the large biomass would have masked trends in the other groups. Overall, study means were 1.4, 1.3, 0.8, 3.7, and 16.4 g AFDW/m^2 for <2, 2-4, 4-8, 8-16 and >16 mm sizes respectively.

ANNUAL BENTHIC AND EPIBENTHIC PLANKTON PRODUCTION BY FEEDING TYPE

In this section we convert benthic plant and animal biomass to annual production in AFDW by applying production/biomass ratios (i.e. turnover rates) available from the literature. Several literature reviews are available and these are included in the Discussion.

We used Edgar's (1990) "general" regression to calculate benthos production per animal-day (P_{ad}) in ug AFDW from inputs of temperature (T in ^oC) in each month and mean animal size (w in ug).

$$P_{ad} = 0.0049\ w^{0.8}\ T^{0.89}$$

We chose Edgar's regression because he used AFDW for biomass, as we did, and daily production related to temperature and animal size. This allowed us to incorporate seasonal changes in temperature and biomass in calculating annual production.

We used our temperature data from 1981-82 (Fig. 9), our mean animal sizes for each size category in each feeding type (Table 8), and our total weight in each size category (M), feeding type, and month (m) (not shown) to calculate monthly production by size and feeding type (P_{sfm})

$$P_{sfm} = P_{ad} \cdot 30.5\ d/m \cdot M/w$$

We assigned zero production for January-March because the temperatures of <2^{o}C probably stopped growth, although negative production was a possibility during these months. We interpolated biomass between months where we lacked data. We calculated average AFDW per animal in each feeding type (O/D, grazer, suspension, predator) and size category in mm (<2, 2-4, 4-8 mm), based on an average of 10 or more samples distributed throughout the study. Because the larger predators were predominately crabs and starfish, and grazers were predominately *Littorina*, average P_{ad} per animal 9-16 mm and >16 mm were calculated using Edgar's equations for crustaceans and molluscs respectively.

crustaceans $\quad P_{ad} = 0.0014\ w^{0.81}\ T^{1.32}$

molluscs $\quad P_{ad} = 0.0066\ w^{0.87}\ T^{0.46}$

The size of *Littorina* was substituted for the few large suspension feeders, mostly *Mytilus*. There were no large O/D.

Similar methods were used to calculate production by epibenthic plankton. Each time period was represented by 12 tows (four replications in three treatment areas). 1981 and 1982 had four sampling periods each. Because most of the animals greater than 8 mm could have escaped the net or were *Littorina* and included in the benthic samples, results for these animals were not included.

For the kelp, *Laminaria longicruris*, in a sheltered area about 5 km from our study site, Gerard and Mann (1979) gave an AFDW/wet weight ratio of 0.15 and an annual production/biomass (P/B) ratio of 2.7 for large plants. In 1981 most of the plant biomass in our study was from large *Laminaria* in the kelp treatment but smaller plants increased in the other two treatments in the next two years.

Although composed of several species (Table 5), the remaining biomass was predominately *Chondrus crispus* and *Fucus* sp. Barron et al. (2003) provided a P/B ratio of 1.1 from a *Fucus serratus* dominated community in southern Norway. Because of the increase in small plants for all macrophytes in the treatment areas, we will assume annual P/B ratios of 2.0, 2.5 and 3.0 for 1981, ‘82, and ‘83 respectively.

Using the (interpolated) monthly biomass for benthos <8 mm and plankton <8 mm, and annual average biomass for benthos >8 mm and macrophytes, gives the estimated production values in Table 9 for each of three treatments. Even if the net captured only one-half the epibenthic plankton, no feeding type had a significantly large biomass compared to benthos. Large grazers (snails) and large suspension feeders (mussels) dominated the benthic production, whereas small animal production was dominated by grazers (*Lacuna*) and O/D (amphipods and mysids). Fig. 16 illustrates the relative production of each feeding type and of macrophytes.

We can also make an educated guess for the fraction of plant production consumed by grazers plus O/D. If grazer plus O/D consumption was 2 (Callow 1977) to 6 (Steele 1974) times their production, then in 1981 consumption was 28-85 g AFDW/m^2 compared to seaweed production of 341 g AFDW/m^2. For 1982, when seaweed production increased to 858 AFDW/m^2, consumption was 26-78 g AFDW/m^2. Likely, most of the seaweed production was exported from the habitat.

BENTHIC ANIMAL-PLANT SPATIAL CORRELATIONS

For each of seven sampling periods, spatial correlations were calculated for animal benthos in g AFDW/m^2 vs. kelp wet weight, vs. other-plant wet weight, and vs. total plant wet weight, all in g/m^2. Animal benthos was divided into sizes of <8 mm, 8-16 mm, and >16 mm in each feeding type. For example, after converting all weights to g AFDW/m^2 of grazers >8 mm from two large quadrats pooled this was correlated with kelp biomass in the same two quadrats. Also, biomass of grazers <8 mm from two small quadrats was correlated with small macrophyte biomass from two small quadrats plus kelp biomass from two large quadrats. For the two larger animal sizes only grazers had enough non-zero values for correlations. Most sampling periods had 18 samples (three shallow and three deep in each of three treatment areas). The last (1983) period had 12 samples.

As noted in the above sections on animal benthos, variation among samples was very high. Correlations were low (Table 10) and few were significant, r>0.46 at P<0.05 with 16 d.f. The higher correlations, considering all dates, were positive for O/D <8 mm vs. other macrophytes, negative for grazers <8 mm vs. kelp, and negative for grazers 8-16 mm vs. kelp. Correlations with total plant biomass were not as strong as for the other two plant categories**.**

FISH STOMACH CONTENTS

Total numbers of stomachs examined for the three treatment areas were pollock-452, cod-225, cunner-118, flounder-36, and others-83. These totals do not include the stomachs collected for the 24 h study in September, 1981. Prey type vs. fish size is reported for pollock and cod. Although only fish with measureable stomach contents were included in this analysis; data presentation includes many zeros because all categories of foods were not present in all stomachs.

For pollock, three prey categories are reported: fish, molluscs, and polychaetes plus crustaceans(excluding crabs) (Fig. 17). Fish prey clearly increased with pollock size with few in pollock less than 20 cm. Prey for pollock <20 cm was dominated by copepods with lesser amounts of ostracods, fish eggs, and polychaetes. Mysids and amphipods were present in all pollock sizes whereas the shrimps, *Crangon* and *Eualis*, were present in fish >25 cm. Molluscs were less important than the other two groups, but were mostly the snail *Skeneopsis* in small fish with increasing numbers of *Lacuna* and *Mytilus* in larger fish.

For cod, three categories are reported: crabs, other crustaceans plus polychaetes, and fish (Fig. 18). *Cancer* crabs were an important diet component in fish over 35 cm. Fish were present at all cod sizes as were crustaceans plus polychaetes. Crustaceans included shrimp and mysids, but not copepods. Diet was more diverse than for pollock.

For each of cod and pollock covariance analysis was used to compare regressions of wet weight of stomach contents vs. fish length among the three treatments. Neither slopes nor intercepts differed among the regressions for either species (Fig. 19). This analysis was limited to the first four time periods before macrophyte recovery following sea urchin mass mortality in order to achieve maximum differences in macrophyte biomass. Empty stomachs were removed from the analysis to reduce the variance about the regressions.

Prey types for less abundant fish species are summarized in Table 11. None of these four species showed conspicuous change is diet choices with fish size. Although 20 families of polychaetes were identified in benthic samples (Moore et al. 1982), fish prey were principally from four families of deposit feeders (Ampharetidae, Flabelligeridae, Pectinariidae, and Nereidae). Among the four fish species in Table 11, cunner had the most diverse diet. Although, by far the greatest variety of prey was seen in a single 58 cm long wolfish. This fish's stomach included carnivores (*Nassarius, Thias, Cancer* crab), suspension feeders (*Mytilus*, *Cerastoderma, Spisula*), O/D (*Nucula, Yoldia, Pagugus*, cumanceans), and algae (eelgrass, kelp, filamentous).

DISCUSSION

CRAB AND LOBSTER TRAPS

Cancer crab catches were about five times higher in kelp than on barrens and the mean CW was about 1 cm larger. This compares to other results from Nova Scotia where rock crab catches and diver counts were both greater in the kelp than the barren habitat (Miller 1989). In another Nova Scotia trapping study Drummond-Davis et al. (1982) concluded rock crab catches were higher in kelp than on similar bottom without kelp.

In this study lobster catch rates at the edge of the kelp-mud interface vs. the barren rock–mud interface were no different. In most cases mean lobster sizes also did not differ between habitats. In eastern Nova Scotia neither lobster catches in traps nor counts by divers differed between kelp on boulder/cobble and barren boulder/cobble habitat (Miller 1989). On the Maine coast trap catches of sublegal lobsters were marginally higher on sediment than on boulder/cobble or bedrock, whereas diver catches in the same areas were much higher on boulder/cobble than on the other two habitats (Dunnington et al. 2005). Diving off Rhode Island, Fogarty (1976) found lobsters in high abundance on boulders, but absent on gravel and sand.

TRAMMEL NETS AND SEINE

Our results agreed with other studies that juvenile pollock spend their 0+ and 1+ years near shore. Assuming size frequency modes represent cohorts, we found 0+ fish grew from 5 to 17 cm from June to December and 1+ fish grew from 18 to 31 cm from May to December before disappearing from catches. Clay et al. (1989) reported spawning on the Scotian shelf from December-February, offshore capture of larvae 6-23 mm from January to May, and then capture of 8 cm juveniles nearshore starting in July. They subsequently captured the 1+ cohort at ~15-30 cm, as we did, but also captured a larger ~30-40 cm cohort in May-June. Juvenile pollock were also reported in moderate to high abundance in nearshore areas in the outer Bay of Fundy and southwest Nova Scotia (MacDonald et al. 1984; Simon and Campana 1987; Black and Miller 1991; Rangely and Kramer 1995).

Here we found fish catches in trammel nets didn’t differ between kelp, removal, and control treatments. This was consistent with previous studies. When *Ascophyllum* was experimentally removed from sections of the intertidal and compared to adjacent areas with *Ascophyllum* intact, Black and Miller (1991) found no difference in number or weight of total fish captured in pop-up seines. Rangeley and Kramer (1995) found no difference in number of juvenile pollock in naturally occurring *Ascophyllum* and algal free areas using a beach seine.

Juvenile cod, but not adults, were moderately abundant to abundant inshore in southwest New Brunswick (MacDonald et al. 1984) and southwest Nova Scotia (Simon and Campana 1987) but not in the intertidal in southwest Nova Scotia (Black and Miller 1991). In this study we caught juvenile and adult cod (11-74 cm) throughout the two year study, except in April. The catch rate was second only to pollock.

The third most abundant species, cunner of mostly 9-12 cm, was prominent from June through October, but absent in April, May, and December. Green and Farwell (1971) observed in the field and laboratory that cunners remained in shallow water, but in shelters and inactive, at temperatures below 5^{o}C. In our study they were not captured below 8^{o}C (Fig. 8). They were among the most abundant species captured by Simon and Campana (1987) and Black and Miller (1991).

Silver hake were present only in August and October, and appeared to be a single cohort of 34-45 cm total length. These fish would have been mature and at least 3+ yrs old (Helser 1996).

Pollock (35%) and cunner (26%) dominated gill net catches in a wave-exposed shallow rocky area in Maine (Ojeda and Dearborn1991). For all fish species combined, catches where highest in July-November and markedly lower in December-June. Fleshy macrophytes were limited to <5 m depth with only coralline algae deeper (Ojeda and Dearborn 1989). Our total catches, sampled April through December, were also lower in spring and late fall but never near zero. Commercial species were caught on all sampling dates: pollock from April-December, cod from May-December, winter flounder from April-October, and silver hake from August-December.

FISH STOMACH CONTENTS

We compare our results for the abundant species with a small selection of the extensive literature on this topic. We assume fish are opportunistic feeders taking whatever is available that they can capture and assimilate. Therefore, we assume differences in diet among locations reflect differences in prey availability.

Among four hauls during a 24 hr. period in the lower Bay of Fundy, MacDonald and Waiwood (1987) found maximum stomach fullness at dusk for winter flounder, ocean pout, and American plaice. Among five hauls in 24 hrs. we found stomach fullness highest at dawn and dusk.

For cod 10-70 cm we observed the weight of crab prey to increase with cod size, fish were present but in low abundance at all sizes, and small crustaceans plus polychaetes were highest for cod 10-35 cm. For the northeast U.S. shelf, amphipods, mysids, and decapods dominated in cod <20 cm whereas fish and decapods were prominent in larger cod. Polychaetes were insignificant (Bowman et al. 2000; Link and Garrison 2002).

For 12-30 cm pollock in a near-shore, hard-bottom area on the New Hampshire coast, Ojeda and Dearborn (1991) reported fish as the dominant prey and crustacea, excluding zooplankton, as the second most important. Bowman et al. (2000) listed euphausids for large pollock only. Leim and Scott (1966) reported euphausids and amphipods as prey for inshore pollock. We found copepods to dominate in pollock less than 20 cm, mysids and amphipods in pollock of all sizes, and fish and shrimp in larger pollock.

Green et al. (1984) listed limpets, horse and blue mussels, and green urchins as the dominant food items for cunner collected in a shallow embayment in Newfoundland. *Lacuna* was a minor component and polychaetes were not listed. We found blue mussels, *Lacuna*, and polychaetes dominant at our sites.

Ojeda and Dearborn (1991) found winter flounder 19-29 cm diet to be entirely of algae in a rocky coastal area of Maine. Bowman et al. (2000) reported predominately polychaetes in fish <16 cm, and polychaetes, anemones and amphipods in larger fish. In flounder from the intertidal and shallow subtidal in the Bay of Fundy gut contents by weight were 40% algae, 18% amphipods, and 11% oligochaetes (Wells et al. 1973). On a sea urchin dominated barrens in Newfoundland, Keats (1990) found food of flounder averaging 34 cm to be dominated by macroalgae, anemones, fish eggs, and sea urchins. In decreasing order of importance we found polychaetes, amphipods, and algae. With the exception of two fish of 7 and 8 cm, the flounder averaged 34 cm with 5 cm standard deviation. Even the small flounder consumed polychaetes and amphipods.

Stomachs of shorthorn sculpin of 19-44 cm in Maine included primarily crustaceans, excluding zooplankton, and echinoderms (Ojeda and Dearborn 1991). We observed decapod and fish prey for fish of similar size.

The similarity in weight of fish stomach contents among the three treatments suggests either the presence of macrophytes didn't affect the quantity of food eaten or fish were foraging was over an area larger than our treatments.

MACROPHYTES AND SEA URCHINS

For a sheltered location we recorded occurrence of benthic algae over a depth gradient and its change over time after removal of grazing sea urchins, first experimentally and then by disease (Table 5, Fig. 10). Dominating the shallow subtidal were *Fucus* as early colonizer and *Chondrus* in the mature kelp treatment. *Laminaria* dominated the deeper portion of the kelp treatment and over time became important in the removal treatment. Many other species were present as noted, and varied on a small spatial scale. Algal zonation has been well documented for eastern Canada (Mann 1972; Pringle and Semple 1980; Miller 1985a; Himmelman 1991).

Algal biomass began recovering in April 1982 even though most urchins were removed experimentally the previous May-June 1981 and the remainder by disease in September-October 1981 (Fig. 10; Miller 1985a). This timing reflected the February-April recruitment of the dominant kelp, *Laminaria longicruris* (Chapman 1984). By June 1983 macrophytes in the control treatment had not attained the biomass of the mature kelp bed, but biomass in the removal treatment was similar. Mann (1973) showed that growth for three kelp species nearly stopped in the summer-autumn and plant biomass decreased by blade erosion. Growth resumed in January and peaked in March-June. Removal of benthic algae by grazing *S. droebachiensis* in Atlantic Canada (Mann 1977; Miller 1985a; Scheibling et al. 1999), Norway (Hagen 1983), and Iceland (Hjorleifsson et al. 1995), and its recovery following removal of sea urchins (see Keats et al. 1990 for review) is well documented. Following experimental removal of sea urchins in February in St. Margarets Bay, about 30 km west of our study area, plots were extensively recolonized by macrophytes by May (Breen and Mann 1976; Chapman 1981). Kelp biomass equaled that in a nearby mature bed by 18 months following removal.

Seaweed refuges from sea urchin grazing are characterized by low salinity, strong wave action, low water circulation, or rock outcrops set in shifting sand (Himmelman et al. 1983). Other organisms also impact kelp abundance. Grazing by the small snail, *Lacuna vincta*, can greatly reduce blade biomass of *Laminaria* (Fralick et al. 1974), but most plants recover (Johnson and Mann 1986). A bryozoan growing on *Laminaria* can make the plant brittle and more susceptible to wave damage (Scheibling et al. 1999). An invasive macrophyte, *Codium fragile,* can out-compete *Laminaria* for space in shallow water (Schmidt and Scheibling 2007).

Natural cycling of benthic algae and sea urchins has been well documented (see above). Mann (1977), Chapman (1981), Wharton and Mann (1981), and Johnson and Mann (1982) concluded that the barren (grazed) state was permanent without a strong outside force controlling the urchin population. On shallow rocky habitat suitable for macroalgae, sea urchins disease and removal by man, either experimentally or by an intense sea urchin fishery, are probably the only agents that can reduce sea urchin grazing sufficiently to allow establishment of a kelp bed (Miller and Nolan 2008).

PRODUCTION

Measuring production of a species in the field is expensive. Many production to biomass (P/B) relationships presented in the literature have been summarized to facilitate calculation of population and community production. For example, Edgar (1990) presented regressions of daily production vs. animal size and temperature for benthic invertebrates. These included regressions for the entire literature set as well as for adults, young, epifauna, infauna crustaceans, and molluscs. He concluded that individual body size explained 92% and temperature 2% of the variance. For marine infaunal populations Schwinghamer et al. (1986) regressed annual P/B against mean animal size in a population and explained 25% of the variation. For marine macrobenthos Robertson (1979) regressed annual P/B against animal life span in years and explained 70% of the variation. For macrofaunal crustaceans Cartes et al. (2002) regressed annual P/B against temperature and mean individual weight to explain 37% of the variation. When a term for benthic vs. suprabenthic was added to the equation, the explained variation increased to 53%. These authors also presented a good review of similar regressions published by others. Cusson and Bourget's (2005) reviewed the largest number of studies for marine macroinvertebrates and provided annual P/B ratios for categories of phylum, feeding type, and substratum. They grouped all the above categories in one stepwise multiple regression with independent variables of life span (71%), mean body mass (1%), water depth (0%), and mean annual temperature (0.3%) to explain 73% of the total variation. In other regressions, including parts of the data set, life span always explained far more of the variation than other independent variables, although life span would no doubt have been correlated to body mass. They gave mean annual P/B ratios of 1.77, 3.37, 4.85, and 0.34 for molluscs, annelids, arthropods, and echinoderms respectively. Converting their biomass units in kJ to AFDW using 239 cal/kJ and 5500 cal/g AFDW, their median animal sizes were 35 mg, 0.44 mg, 0.87 mg, and 239 mg AFDW for molluscs, annelids, arthropods and echinoderms respectively. The relatively large size and long life span for the echinoderm populations in the sample would contribute to the low P/B for this group. They also gave P/B ratios of 2.54, 4.94, 1.82, 2.81, and 3.41 for deposit feeders, omnivores, filter (suspension) feeders, grazers, and predators, respectively.

We see that P/B ratios have differed among reviews. The literature each employed was different and some of the independent variables (e.g. temperature, depth, infauna, epifauna, animal size, and age) in the regressions were different. For comparison, P/B ratios have been standardized to 5 mg AFDW when the data presentation permitted (Table 12). Comparing ratios for similar sized animals from different authors suggests that our calculated production values would not have differed greatly had we used ratios from different authors.

Total invertebrate benthic production was about 23 g AFDW/m^2 in both 1981 and 1982. Taylor (1998) reported community production for a shallow hard bottom reef in New Zealand. For animals retained in a 0.5 mm sieve, excluding fish and large decapods, annual productivity was 47 g AFDW/m^2 and biomass was 27 g AFDW/m^2. Grazing gastropods and small crustacea comprised 79% of production and 47% of biomass. For animals large enough to be collected by hand in a shallow hard bottom habitat about 20 km from our study site, Miller et al. (1971) reported annual production of 17.6 g AFDW/m^2, of which 71% was sea urchins. This production was close to 19 g AFDW/m^2/yr for animals >8 mm in this study.

Our epi-benthic plankton production of 0.1 g AFDW/m^2 in both years was insignificant compared to benthic production.

If we sum grazer and O/D production and multiply by a ratio of consumption to production, we see that seaweed production exceeded on site consumption by an order of magnitude. Thus, macrophyte production must be exported. Export of seaweed production has been previously supported by several authors including Miller et al. (1971), Mann (1973), Chapman (1987), and Fredriksen (2003). This contribution would be lost in sea urchin dominated barrens (Chapman 1981).

BENTHIC ANIMAL-PLANT SPATIAL CORRELATIONS

The low correlations overall (Table 10) between biomass of macrophytes and benthic animals were unexpected. The positive correlations of <8 mm O/D with “other macrophytes” were perhaps because the dense low turf of *Chondrus* and *Fucus* were better suited to mysids and amphipods. The negative correlation of <8 mm grazers with kelp was a surprise because *Lacuna* clearly grazed down kelp biomass during the summer. Grazers 8-16 and >16 mm had negative and no correlation respectively with kelp. Dominant animals in both these large sizes were periwinkles (*Littorina* sp.) with apparently little preference for plant community. *Littorina* prefer ephemeral algae such as diatoms and *Enteromorpha* and have a low preference for the kelps, *Fucus*, and *Chondrus* (Lubchenco 1978). The high spatial variability in plant density and the practice of combining two randomly selected quadrats in each plant and benthos sample may have masked some of the spatial correlation.

Other authors have shown benthos abundance to be correlated with habitat complexity. Biomass of small gastropods and crustaceans on New Zealand sea urchin barrens was 16.1 g AFDW/m^2 (29% small crustaceans) compared to 28.4 g AFDW/m^2 (96% small crustacean) in a dense bed of small macrophytes (Taylor 1998). At a wave exposed location off New Hampshire, Whitman (1985) used an air-lift sampler to collect benthos in a bed of horse mussels (*Modiolus modiolus*) and on similar substrate without mussels. Both areas were sampled before and after the kelp and red algal understory were removed by sea urchin grazing. The mussel bed had similar species rank order and similar densities of benthos (488 and 352 animals/0.25 m^2) before and after grazing. However, bottom without mussels had markedly reduced densities (1570 vs. 415 animals/0.25 m^2) and species diversity after it was grazed. Mussels provided shelter from decapod and fish predators. Ojeda and Dearborn (1989) did similar work at a wave exposed site on the Maine coast, monitoring fauna at 5, 10, and 18 m depths. Macrophytes were confined to less than 5 m depth by sea urchin grazing. Sea urchins and horse mussels dominated the biomass. Urchins decreased with depth and horse mussels increased. The other benthic fauna, composed of crustaceans, molluscs, and polychaetes, were most diverse at 18 m within horse mussel beds. Sebens (1985) and Steneck (1986) also studied the rocky bottom fauna on the New England coast. All these authors presented densities and or biomass by species but not feeding types or size groupings that could be compared to our results. Also, no beds of horse mussels were present in this study.

In the Gulf of St. Lawrence estuary Himmelman et al. (1983) observed recovery of macroalgae and increased abundance of molluscs and crustacea following removal of urchin grazers. An unaltered community in the same area remained dominated by sea urchins and sea anemones. Polychaete biomass was similar in both areas.

SUMMARY

Cancer crabs prefer hard bottom with kelp to hard bottom without macrophytes. The most abundant fish larvae during June through October were the non-commercial species of cunner and gunnel. Juvenile pollock from 4 cm were very abundant and grew quickly. On the scale of sampling employed, there was little or no correlation between plant biomass and biomass of fish, fish gut contents, epibenthic plankton, or benthic animals. Epibenthic biomass was lower over mud, however. Benthic plant and animal biomass were highly variable. Among predators, omnivores/detritovores (O/D), grazers, and suspension feeders <16 mm, grazers had the highest biomass. Among size classes of <2, 2-4, and 4-8 mm when all feeding types were summed, the largest biomass was in the smallest size interval. The largest size classes of 8-16 and >16 mm had the greatest biomass overall. Because these relationships did not change during 3 years of study, and because correlations of animal to the more variable plant biomass were lacking, the sampling employed appears to have been a robust representation of the fauna. Production per m^2 was in the approximate ratio of 1:10:300 for trophic levels of predators, grazers + suspension feeders + O/D, and macrophytes. Production of epi-benthic plankton was <1% of benthic production. Fish were present throughout the sampling period of April through December.

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TABLES

Table 1. Collection dates for each sample type, and number of samples (n) for some types.

Year	Fish size	Trammel nets Fish guts	Prey[1]	Benthos <8 & >8 mm	Epibenthic plankton	Fish <8 mm in plankton	Seine	Crab or lobster traps
1981	May 27 (3)	May 27	size+type					
	May 28 (3)	May 28		May 29 (8)				
	May 29 (3)			Jun. 5 (12)				
	Jun. 4 (3)			Jun. 9 (4)	Jun. 4,9 (12)	Jun. 4,9	Jun. 18	
	Jul. 2 (3)	Jul. 2	size+type	Jun. 19 (12)	Jul. 2,7 (16)	Jul. 2,7	Jul. 13	
	Jul. 6 (3)							
	Jul. 7 (3)	Jul. 7						
	Jul. 8 (3)							Aug. 10 (16)
	Aug. 17 (3)	Aug. 17	type only	Aug. 26 (20)	Aug. 1,22,24	Aug. 17,20,24		Aug. 11-12 (16)
	Aug. 20 (3)	Aug. 20	type only	Aug. 28 (16)	(16)			Aug. 13 (16)
	Aug. 25 (3)	Aug. 25	type only					Aug. 20 (21)
	Aug. 26 (3)		type only					Aug. 24 (21)
	Oct. 15 (3)	Oct. 15	type only			Oct. 15,22		Sept. 2 (20)
	Oct. 20 (3)	Oct. 20	type only					Oct. 14 (20)
	Oct. 28 (3)	Oct. 28	type only					Oct. 15,16 (20)
	Oct. 30 (3)							Nov. 4-5 (20)
				Nov. 24 (12)	Nov. 27,			Nov. 5-6 (20)
	Dec. 1 (3)	Dec. 1	type only	Nov. 25 (12)	Dec. 1 (16)	Dec. 2		Nov. 9-10 (16)
	Dec. 7 (3)	Dec. 7	type only					Nov. 10-11 (16)
	Dec. 11 (3)	Dec. 11	type only					Nov. 12-13 (21)
	Dec. 21 (3)	Dec. 21	type only	Dec. 21 (12)				Nov. 13-14 (21)
1982	Mar. 30 (3)							
	Mar. 31 (3)							
	Apr. 5 (3)			Apr. 20 (10)	Apr. 2,6 (16)			
	Apr. 6 (3)			Apr. 23 (10)				
	Apr. 30 (3)			Apr. 26 (12)			Jun. 9-10	
	May 4 (3)	May 4	size+type	May 5 (4)	May 5,7 (16)			
	May 6 (3)	May 6	size+type					
	May 10 (3)	May 10	size+type					
	May 25 (3)	May 25	size+type					
	May 31 (3)	May 31	size+type					
	June 3 (3)	June 3	size+type		Jun. 3,9 (16)			
	June 8 (3)	June 8	size+type					
	Aug. 17 (3)	Aug. 17			Aug. 17,30 (16)			
	Aug. 19 (3)	Aug. 19		Aug. 19 (12)				
	Aug. 26 (3)	Aug. 26		Aug. 25 (12)				
	Sept. 1 (3)	Sept. 1		Sept. 2 (12)				
1983				Jun. 22 (8)				
				Jun 24 (12)				

Table 1 (cont'd). Collection dates for each sample type, and number of samples (n) for some types.

Year	Fish size	Trammel nets: Fish guts	Trammel nets: Prey[1]	Benthos <8 & >8 mm	Epibenthic plankton	Fish <8 mm in plankton	Seine	Crab or lobster traps
				Jun 28 (12)				
				Jul. 5 (4)				
1984				Jun. 21 (12)				
				Jun. 22 (12)				

[1]Prey type from gut contents, feeding type or taxonomic grouping.

Table 2. Chi-square comparing total catch per treatment and ANOVA comparing mean size per treatment for catches of cancer crabs in crab traps and lobsters in lobster traps. Crab were set on barrens and in dense kelp (A vs. B and C vs. D), and in the three experimental areas. Lobster traps were set at the rock-mud interface at the same locations.

			Soak	Traps per	Total catch per treatment			Chi-		Mean size per treatment (cm)				
Species	Areas	Date	time (h)	treatment	Control	Kelp	Removal	square	P	Control	Kelp	Removal	F	P
Cancer	A&B	14 Oct.	4	10	6	22		34.6	<0.01	8.6	9.4		6.2	<0.05
		15-16 Oct.	20	10	8	45								
	C&D	10 Aug.	2	8	13	37		79.1	<0.01	7.6	8.6		24.6	<0.01
		11-12 Aug.	13	8	4	33								
		13 Aug.	5	8	14	80								
	Exper.	20 Aug.	6	7	11	27	22	29.5	<0.01	8.1	8.9	8.5	6.9	<0.01
		24 Aug	7	7	17	53	19							
Lobster	A&B	4-5 Nov.	24	10	15	11		1.6	>0.1	6.3	6.8		2.7	>0.1
		5-6 Nov.	24	10	14	22								
	C&D	9-10 Nov.	24	8	20	35		0.6	>0.1	7.3	7.5		1.9	>0.1
		10-11 Nov.	25	8	15	10								
	Exper.	12-13 Nov.	24	7	16	12	16	0.5	>0.1	6.7	7.3	7.2	3.8	<0.05
		13-14 Nov.	24	7	16	20	11							

Table 3. Taxa providing most AFDW in epibenthic plankton by feeding type and date.
.

Date	Treatment	Susp.	Predator	Grazer	Omnivore/detritovore
4-9/6/81	silt		no collections on this date		
	control	-	rock gunnel	*Lacuna*	mysid, *Gammarus*, shrimp
	removal	-	rock gunnel	*Lacuna*	*Gammarus*, shrimp
	kelp	-	rock gunnel, scaleworm	*Lacuna*, *Skeneopsis*	*Gammarus*, mysid, shrimp, *Nereis*
2-7/7/81	silt	*Crenella*	dog whelk, scale worm	-	shrimp, cumaceans, mysids
	control	-	nudibranchs	-	shrimp, mysid, *Gammarus*
	removal	*Mytilus*	rock gunnel, grubby	-	mysid, shrimp, *Gammarus*
	kelp	-	starfish, gunnel, scaleworm	*Lacuna*	mysid, shrimp, *Gammarus*, *Nereis*
1-22-24/8/81	silt	-	-	-	*Lacuna* mysid, shrimp, isopod
	control	-	-	-	*Lacuna* mysid, shrimp, isopod
	removal	-	-	-	mysid, isopod, shrimp
	kelp	-	cunner, scale worm mud snail	-	mysid, *Gammarus*, shrimp, blood star
27/11-1/12/81	silt	-	cunner, dog whelk	-	shrimp, mysid, isopod, *Nucula*, *Gammarus* (*Crangon*)
	control	-	-	*Lacuna*	mysid, hermit crab, *Gammarus*
	removal	*Mytilus*	cunner, gunnel	*Lacuna*, limpet	mysid, shrimp, hermit crab
	kelp	tunicate	cunner, starfish	*Lacuna*	shrimp, mysid, *Gammarus*
2-6/4/82	silt	-	rock gunnel, crab larvae	-	shrimp (*Crangon*, *Eualus*)
	control	-	-	*Lacuna*, limpet	*Gammarus*, shrimp, *Hydrobia*
	removal	-	-	*Lacuna*, *Littorina* limpet	*Gammarus*, shrimp, *Hydrobia*
	kelp	-	stauromedusae	*Lacuna*, *Skeneopsis*	mysid, shrimp (I), *Gammarus*
5-7/5/82	silt	-	-	*Lacuna*	shrimp (*Crangon*, *Eualus)*, *Gammarus*, mysid
	control	*Mytilus*	rock gunnel, cunner stauromedusae	*Lacuna*	*Gammarus*, *Pagurus*, shrimp

Table 3 cont.

	removal	*Mytilus* *Hiatella*	rock gunnel, caprellid	*Lacuna*	shrimp, *Gammarus*
	kelp	tunicate	rock gunnel, *Asterius* nudibranch	*Lacuna*	shrimp, *Gammarus*
3-9/6/82	silt	-	-	-	shrimp
	control	-	cunner	*Lacuna*	*Gammarus*
	removal	*Mytilus*	cunner, pollock rock gunnel	*Lacuna*	shrimp, *Gammarus*, mysids
	kelp	cockle	pollock, rock gunnel, *Asterius*	-	shrimp, mysid, *Gammarus*
17-30/8/82	silt	-	-	-	shrimp
	control	-	lumpfish	*Lacuna*	mysids,shrimp
	removal	-	lumpfish	*Lacuna*	mysids, shrimp, *Gammarus*
	kelp	-	rock gunnel	-	mysids, shrimp, *Gammarus*, blood star

Table 4. Fish species and total number captured by three trammel net hauls on each of 36 dates in 1981 and 1982.

Common name	Genus-species	Total no. captured
Little skate	*Raja erinacea*	8
American eel	*Anguilla rostrata*	1
Atlantic herring	*Clupea harengus*	3
Blueback herring	*Alosa aestivalis, A. pseudoharengus*	9
Smelt	*Osmerus mordax*	5
Atlantic cod	*Gadus morhua*	296
Haddock	*Melanogrammus aeglefinus*	1
Silver hake	*Merluccicus bilinearis*	81
Atlantic tomcod	*Microgadus tomcod*	19
Pollock	*Pollachius virens*	1098
White hake	*Urophycis tenuis*	1
Squirrel hake	*Urophycis chuss??*	3
Ocean pout	*Macrozoarces americanus*	2
Cunner	*Tautogolabrus adspersus*	171
Wolffish	*Anarhichas sp*	2
American sand lance	*Ammodytes americanus*	1
Sea robin	*Prionotus* sp.??	1
Sea raven	*Hemitripterus americanus*	11
Grubby	*Myoxocephalus aenaeus*	15
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	3
Shorthorn sculpin	*Myoxocephalus scorpius*	18
Striped sea snail	*Liparis liparis*	3
Winter flounder	*Pseudopleuronectes americanus*	49

Table 5. Predominant algal species at depth in three treatments in August 1981 and August 1982.

Water depth (m) (below mlw)	Control	Removal	Kelp
1981			
0-1.0	*Fucus vesiculosus*	*F, vesiculosus*	*Chondrus crispus*
1.0-2.0	*C. crispus* rock	*C. crispus,* *F. edentatus*	*C. crispus*
2.0-2.5	rock	*Cordaria flagelliformis*	*C. crispus*
2.5-3.0	*C. flagelliformis*	*Cystoclonium purpureum*	*C. crispus*
3.0-3.5	*C. purpureum*	*C. purpureum*	*Chaetomorpha linum*
3.5-5.5	*C. purpureum* *C. flagelliformis*	*Laminaria longicruris*	*L. longicruris* *Desmarestia aculeata*
5.5-6.5	*rock/sand*	sand	sand
1982			
0-1.0	*F. vesiculosis*	*F. vesiculosus*	*F. vesiculosus*
1.0-2.0	*F. edentatus C. crispus*	*F. edentatus*	*C. crispus, C. purpureum*
2.0-3.0	*C. purpureum,* *C. crispus* *Cordaria falgelliformis*	*C. purpureum* *C. flagelliformis*	*L. longicruris* *Saccorhiza dermatodea*
3.0-4.0	*L. longicruris* *Dictiosiphon sp.*	*L. longicruris* *S. dermatodea*	*L. longicruris*
4.0-5.0	*Dictyosiphon* sp. *Polysiphonia* sp.	*L. longicruris* *S. dermatodea* *D. aculeate*	*L. longicruris* *Polysiphonia* sp.

Table 6. A. Two-way ANOVA for benthos <8mm in mg AFDW/m^2. Two depths and four feeding types were compared within each of three treatments. Biomass values were first transformed to ln(x+1) and all dates were replications in a depth x feeding type classification. B. Geometric means (back- transformation of transformed means) by treatment area, depth, and feeding type.

A.

		Control		Removal		Kelp	
Source	df	msq	P	msq	P	msq	P
Depth	1	22.9	<0.01	30.3	<0.01	34.0	<0.01
Feeding type	3	5.8	0.10	11.5	<0.01	62.6	<0.01
Interaction	3	5.2	0.13	4.0	0.19	1.9	0.66
Error	136	2.7		2.5		3.6	

B

	Control		Removal		Kelp	
	Shallow	Deep	Shallow	Deep	Shallow	Deep
Suspension	339	109	164	55	147	41
Predator	310	323	272	239	845	550
Grazer	658	122	749	132	212	50
O/D	632	411	449	218	1603	749

Table 7. Probability of no significant difference between biomass (AFDW/m^2) of benthos >8 mm in shallow and deep halves of transects. Data were transformed by $\log_{10}$(X+10 mg). O/D biomass was too low to compare.

	Feeding type		
Area	Suspension	Predator	Grazer
Control	0.65	0.37	0.01
Removal	0.02	0.01	0.01
Kelp	0.02	0.49	0.37

Table 8. Mean animal weights (mg AFDW) for different sizes (mm) and feeding types of benthos and epibenthic plankton based on ≥10 weights taken from 10 dates in 1981-82.

Benthos				Plankton			
		AFDW(mg)				AFDW (mg)	
Feeding type	Size (mm)	Mean	SD	Feeding type	Size (mm)	Mean	SD
O/D	<2	1.9	0.9	O/D &	<2	0.7	0.6
	2-4	11.2	7.2	predator	2-8	10.4	7.8
	4-8	92.1	46.5	suspension	<2	0.2	0.1
predator	<2	1.1	0.6	& grazer	2-8	1.1	0.6
	2-4	4.6	1.7				
	4-8	41.3	22.7				
suspension	<2	0.8	0.4				
	2-4	1.7	1.1				
	4-8	13.2	16.7				
grazer	<2	0.8	0.4				
	2-4	2.6	0.9				
	4-8	10.3	5.0				
crabs and	8-16	165	37				
starfish	>16	1893	1960				
Littorina	8-16	395	158				
	>16	590	166				

Table 9. Annual production of benthos and plankton (mg AFDW/m^2).

Feeding type	Annual benthic production 1981	1982	1983	Annual plankton production size	1981	1982
macrophytes	341,100	858,000	1,322,200			
grazers-size						
≤2	394	666	2941	≤2	8	5
2-4	316	529	721	2-8	9	25
4-8	83	146	279			
8-16	4166	2282	2836			
>16	7853	7660	8167			
totals	12812	11283	14944		17	30
O/D-size						
≤2	841	881	1012	≤2	44	68
2-4	339	589	694	2-8	18	18
4-8	137	162	315			
8-16	4	0	30			
>16	0	3	14			
totals	1321	1635	2025		62	86
suspension feeders-size						
<2	330	360	790	≤2	1	1
2-4	536	160	691	2-8	2	1
4-8	85	153	1044			
8-16	372	120	68			
>16	5647	7417	1265			
totals	6970	8210	3858		3	2
predators-size						
≤2	371	415	405	≤2	2	1
2-4	415	457	811	4-8	20	7
4-8	169	305	246			
8-16	128	152	120			
>16	770	1100	381			
totals	1853	2014	1557		22	8

Table 10. Correlation coefficients between plant (g/m^2 wet weight) and benthic animal (g/m^2 AFDW) biomass for four feeding types in seven sampling periods. “Other” is macrophytes other than kelp and “∑” is all macrophytes. Samples from the three treatment areas were grouped.

	29/5-19/6 1981			26-28/8 1981			24/11-21/12 1981			20/4-5/5 1982		
Feed type	Kelp	Other	∑	Kelp	Other	∑	Kelp	Other	∑	Kelp	Other	∑
<8 mm												
suspension	-0.27	0.13	-0.11	-0.39	0.19	-0.17	-0.21	-0.06	-0.17	-0.03	0.32	-0.16
predator	-0.12	0.29	0.07	0.02	0.05	0.04	0.49	0.69	0.77	0.13	0.10	0.15
grazer	-0.39	0.10	0.20	-0.29	0.28	-0.05	-0.32	-0.08	-0.08	-0.09	0.31	0.10
O/D	-0.05	0.45	0.19	-0.25	0.42	0.05	0.13	0.73	0.58	0.08	0.65	0.42
8-16 mm												
grazer	-0.31	-0.27	-0.34	-0.30	0.16	-0.11				-0.26	0.13	-0.12
>16 mm												
grazer	-0.09	-0.22	-0.17	-0.03	0.29	0.13				0.04	-0.15	0.11

	19/8-2/9 1982			22/6-5/7 1983			21/6-22/6 1984		
Feed type	Kelp	Other	∑	Kelp	Other	∑	Kelp	Other	∑
<8 mm									
suspension	-0.37	-0.15	-0.36	0.50	-0.20	0.48	-0.09	-0.01	-0.11
predator	0.45	-0.25	0.08	-0.43	0.70	-0.02	-0.12	0.56	0.21
grazer	-0.17	-0.04	-0.14	-0.46	0.09	-0.51	-0.40	0.53	-0.14
O/D	0.23	0.77	0.65	-0.12	0.58	0.28	-0.05	0.19	0.06
8-16 mm									
grazer	-0.26	-0.15	-0.28	-0.30	0.25	-0.19	-0.29	-0.32	-0.55
>16 mm									
grazer	0.18	0.14	0.22	0.0	0.02	-0.22	-0.33	0.65	0.01

Table 11. Common prey of common fish species other than cod and pollock.

Fish species	Length (cm)	Prey feeding types	Prey
Winter flounder	9-43	O/D	polychaetes, amphipods, algae
Cunner	9-35	grazer, suspension	*Lacuna*, *Mytilus*, polychaetes
Shorthorn sculpin	17-35	predators	cancer crabs, fish
Sea raven	20-45	predators	fish (mostly gunnel)

Table 12. Comparative annual P/B ratios among studies using benthic invertebrates. The average animal size was set at 5 mg AFDW when a regression equation including animal size was provided.

Biotype	P/B	Units	Reference
molluscs	2.9	2 yrs old[1]	Robertson (1979)
general	2.3	5 mg[2]	Banse and Mosher (1980)
general	1.6	5 mg	Schwinghamer et al. (1986)
general	1.8	5 mg	Edgar (1990) and this study
crustaceans	1.5	5 mg	" " " "
molluscs	1.7	5 mg	" " " ""
epifauna	1.9	5 mg	" " " ""
general	1.8	2 mg	Brey (1990)
molluscs	1.1	6 mg	"
crustaceans	4.0	1 mg	"
polychaetes	3.4	2 mg	"
crustaceans	2.0	5 mg	Cartes et al. (2004)
molluscs	1.8	35 mg	Cusson and Bourget (2005)
annelids	3.4	0.4 mg	" "
arthropods	4.8	0.9 mg	" "
echinoderms	0.3	239 mg	" "

[1]P/B regressed against age
[2]P/B regressed against size at maturity

FIGURES

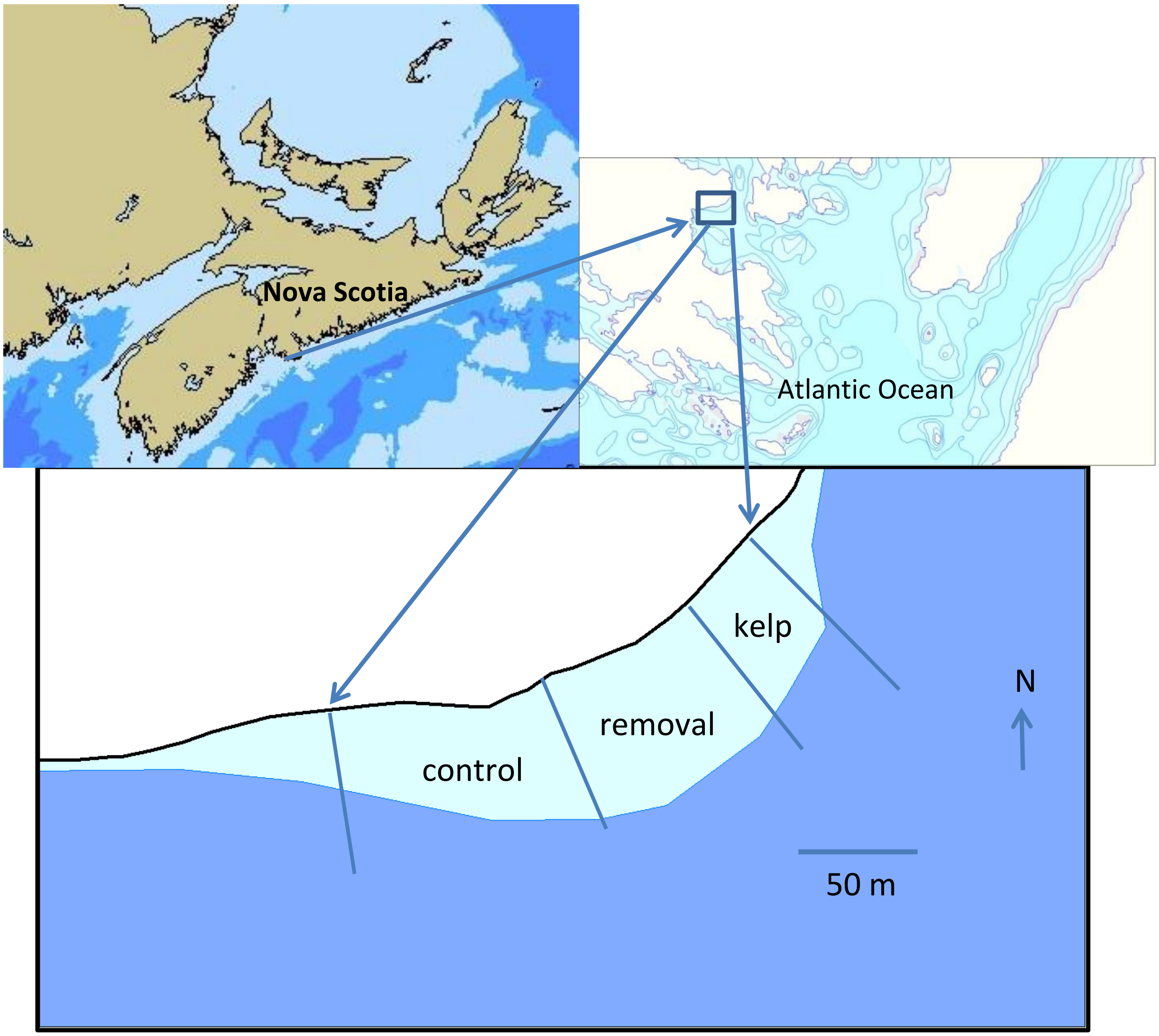


Fig. 1. Map of study area. Experimental treatments are mature kelp bed, sea urchins removed, and control with sea urchins remaining.

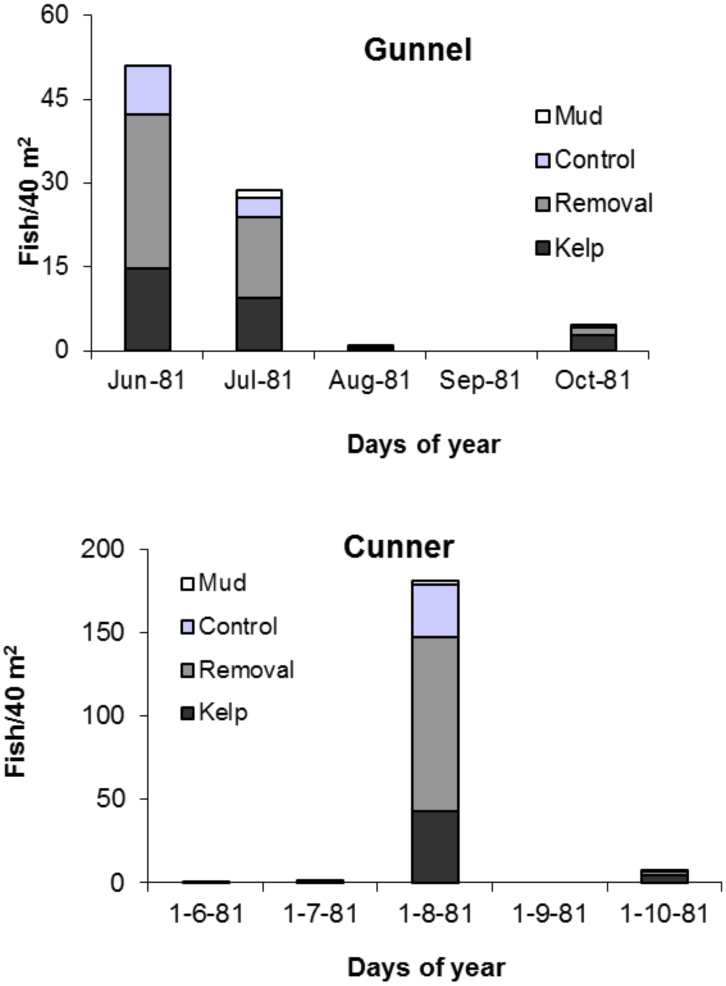


Fig. 2. Rock gunnel and cunner density/40 m^2 from epi-benthic plankton samples.

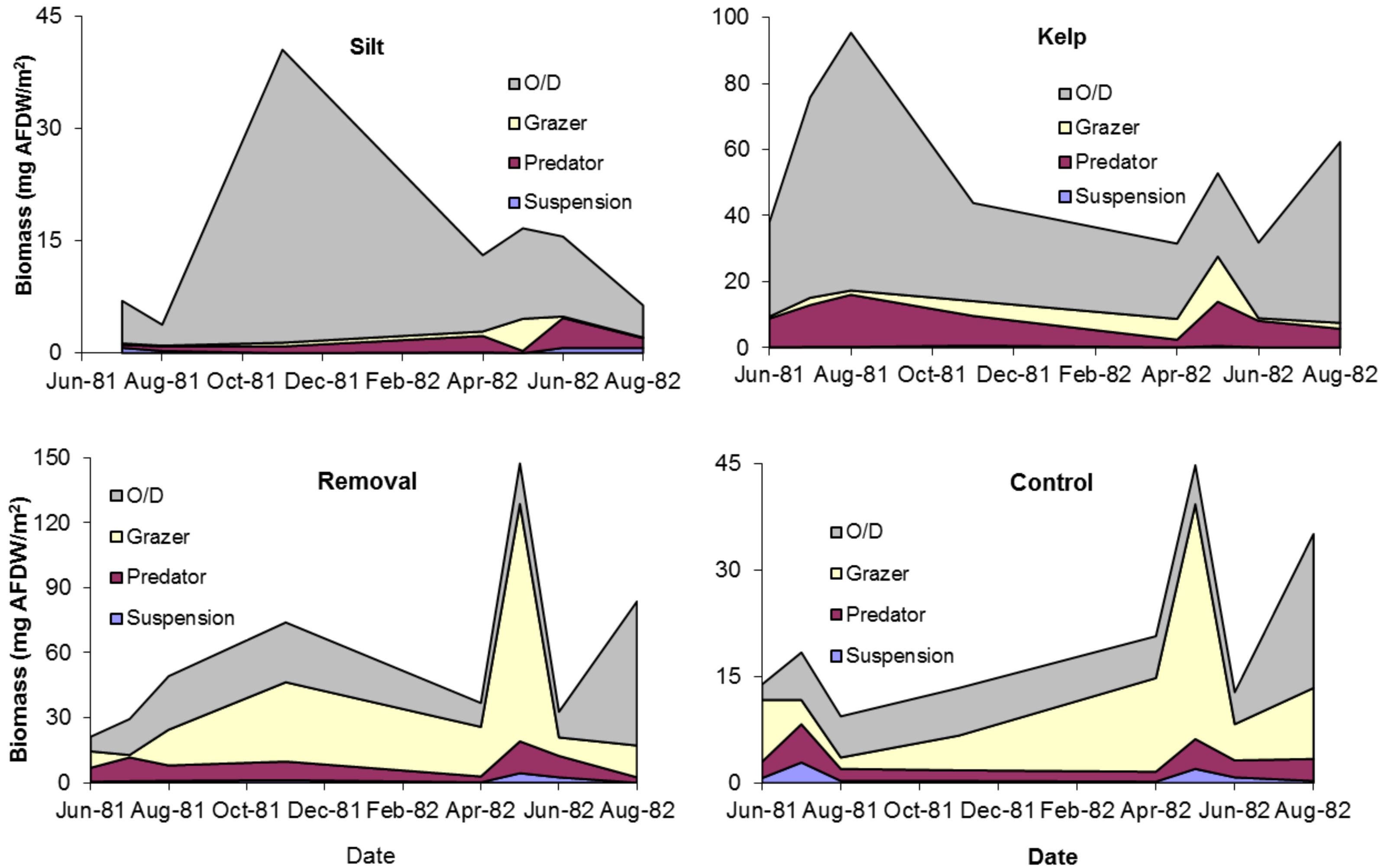


Fig. 3. Biomass (mg AFDW/m^2) from epibenthic plankton samples, by treatment area and feeding type.

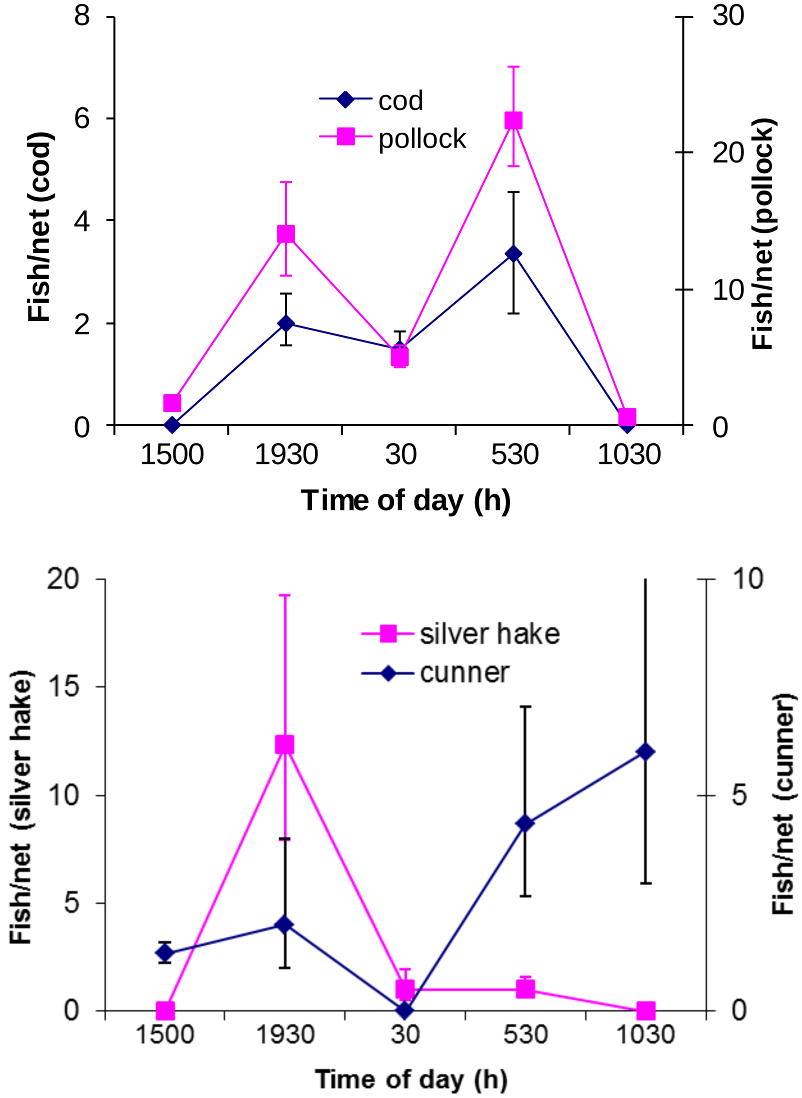


Fig. 4. Mean number fish per trammel net at five times during 24 hrs. Error bars are standard error of the mean calculated from ln(x+1) then back transformed to a fraction of the mean.

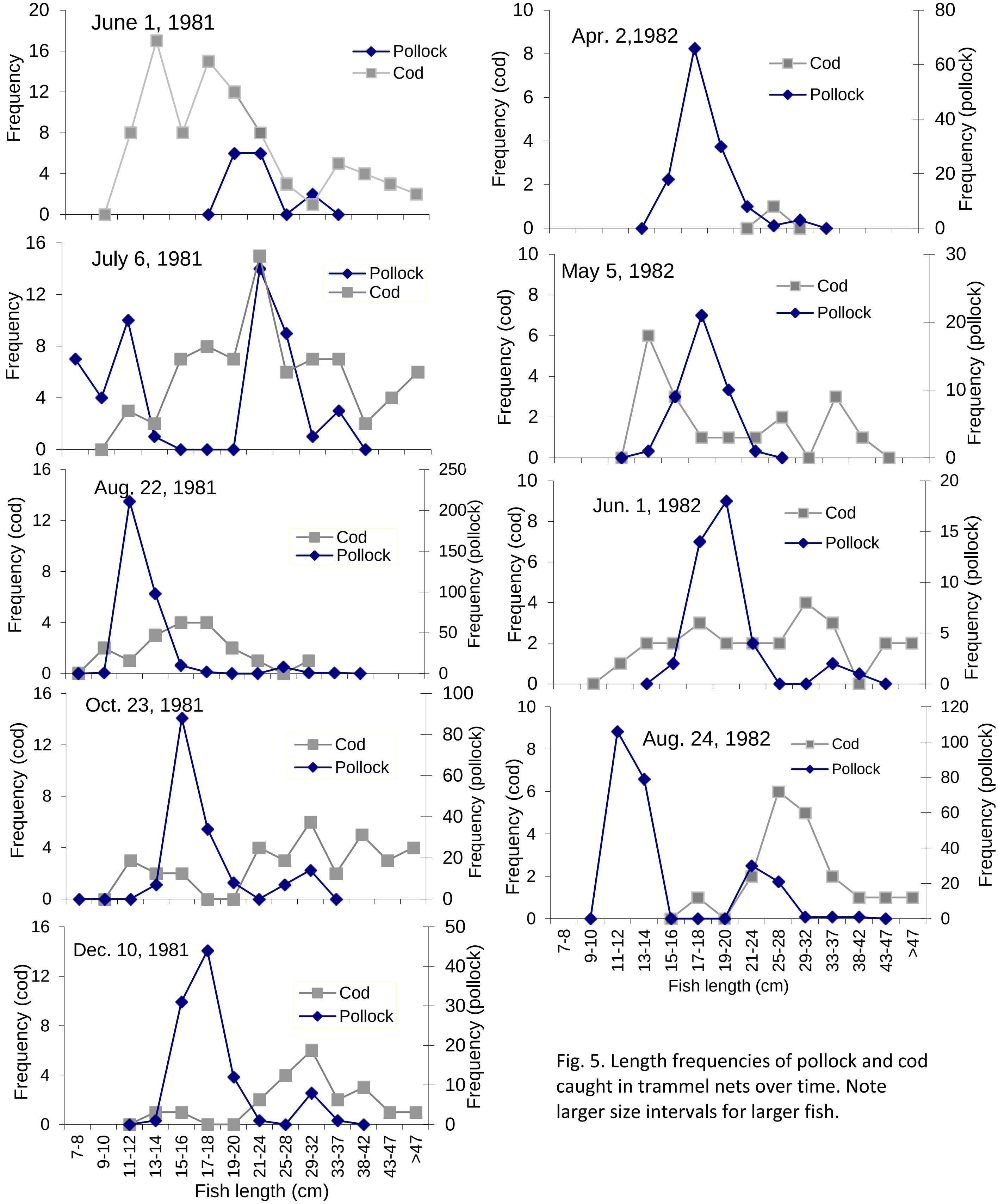


Fig. 5. Length frequencies of pollock and cod caught in trammel nets over time. Note larger size intervals for larger fish.

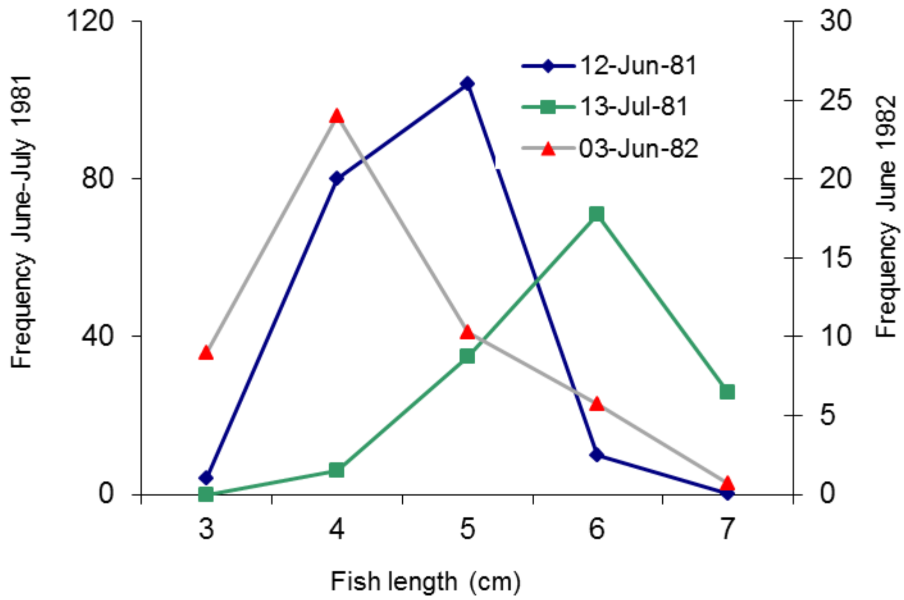


Fig. 6. Length frequencies of pollock captured in a beach seine.
Each point is the mean of three hauls.

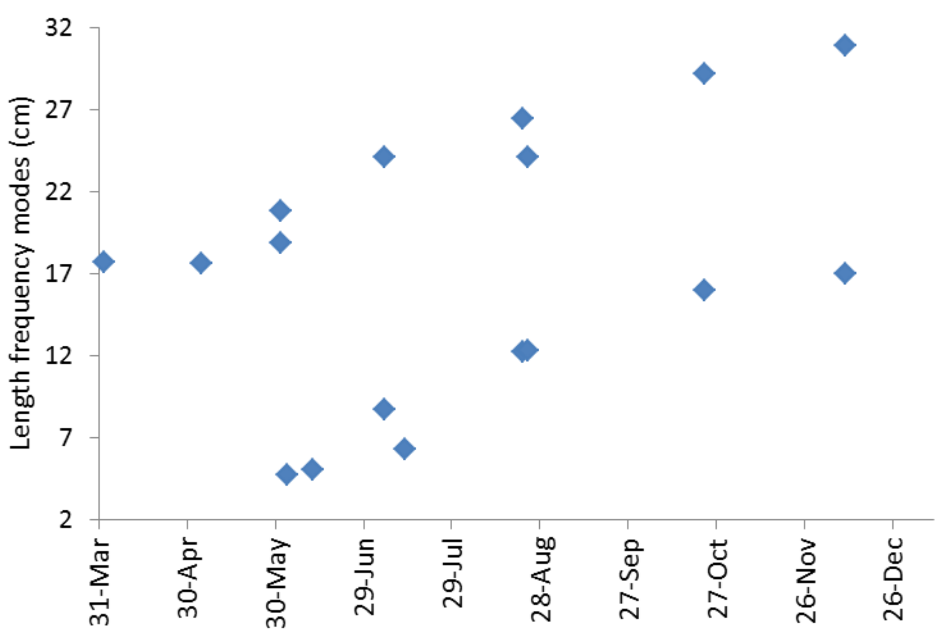
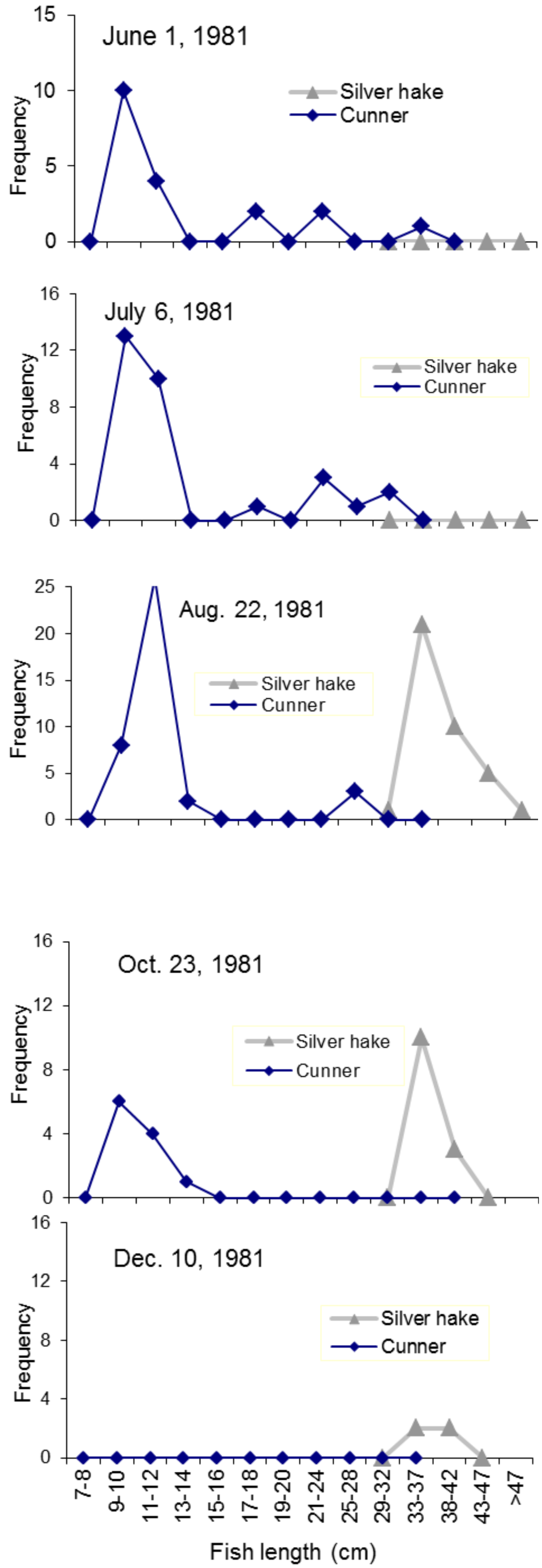


Fig. 7. Centers of modes of pollock length frequency from both trammel net and seine hauls during 1981 and 1982 illustrating age/size cohorts.



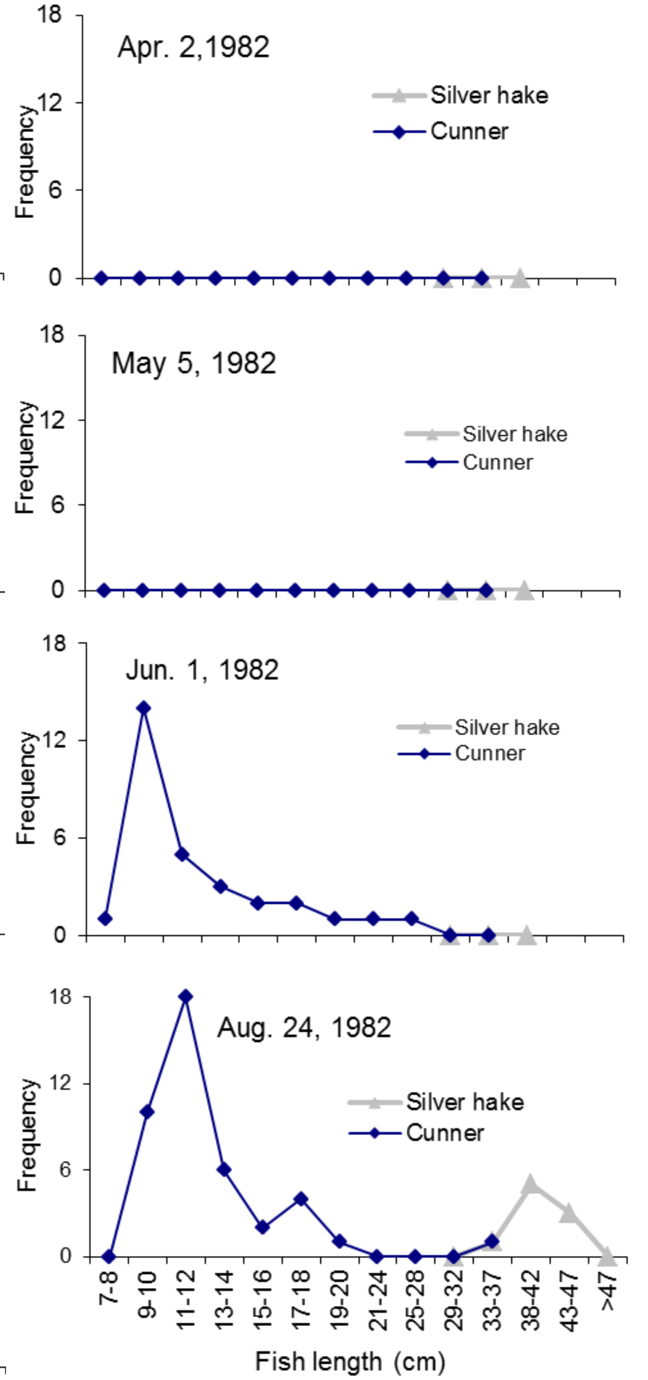


Fig. 8. Length frequencies over time for silver hake and cunner caught in trammel nets. Note larger size intervals for larger

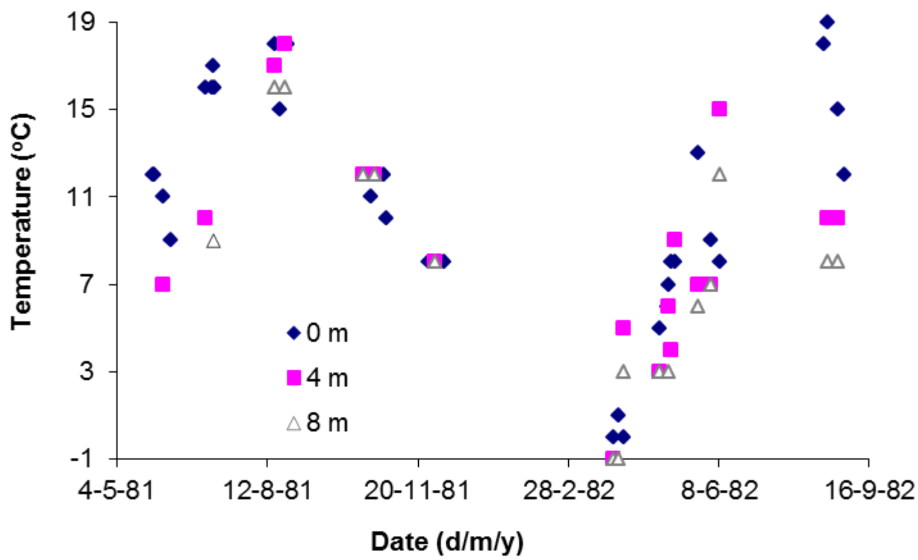


Fig. 9. Temperatures at three depths taken on dates of plankton and trammel net sampling.

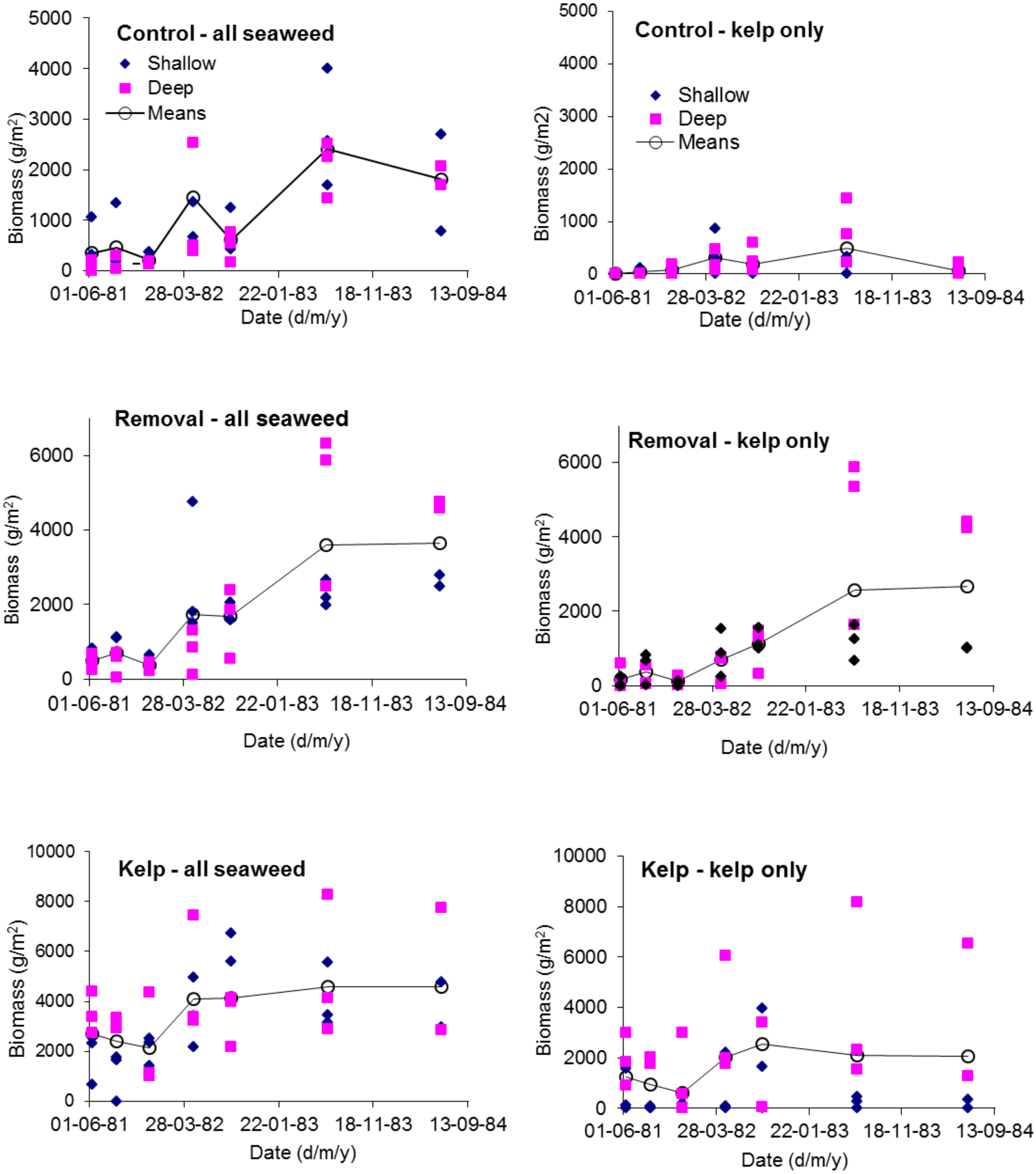


Fig. 10. Biomass (g wet weight/m^2) of all macrophytes and of kelp only for the shallow and deep portions of transects in each treatment. Line connects means for each date.

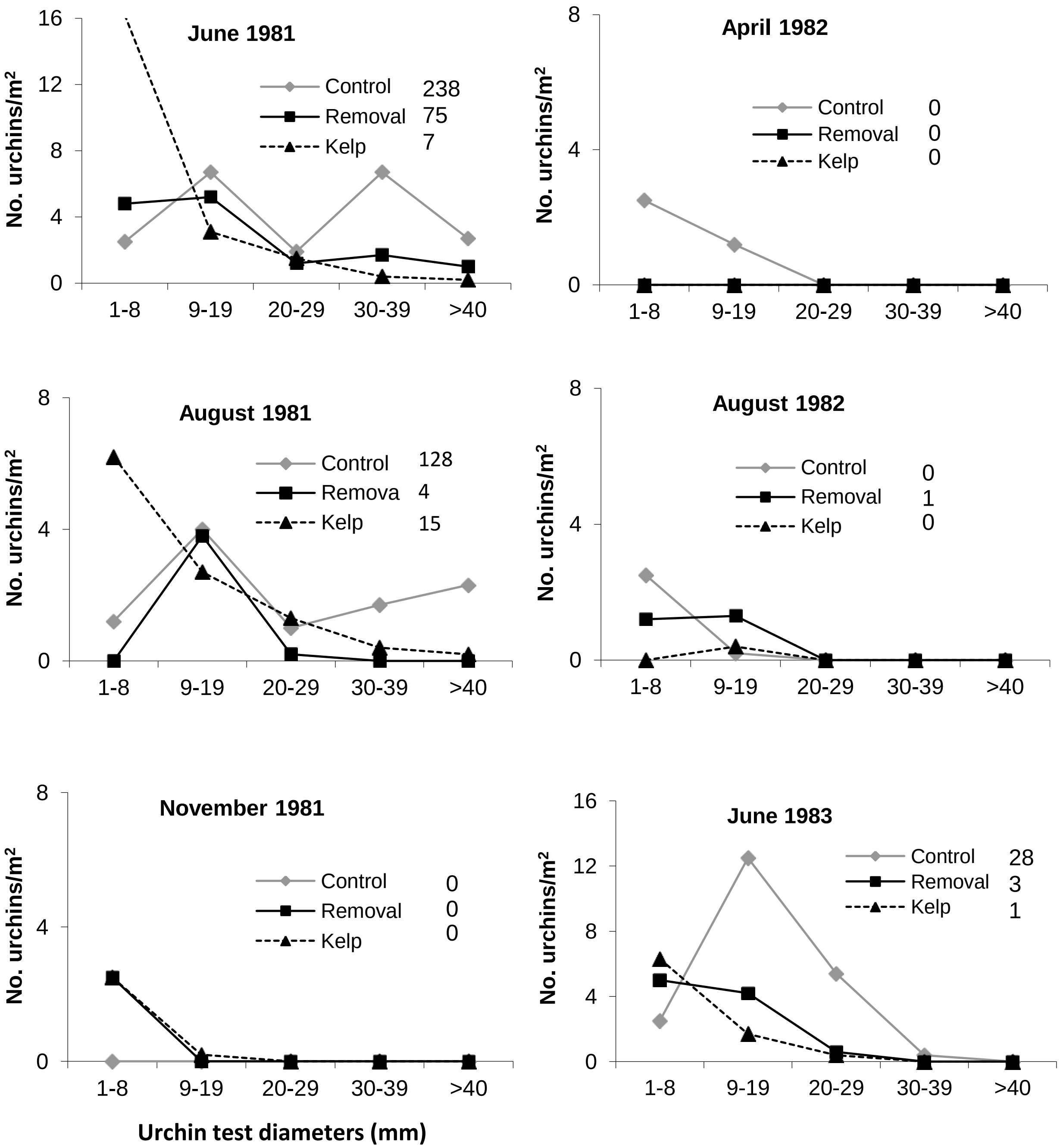
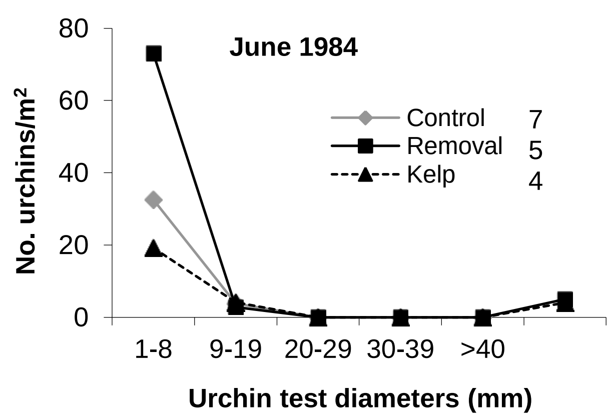


Fig. 11. Sea urchin density (no./m^2) by test diameter (mm) and live weight (g /m^2) in each of three treatments.



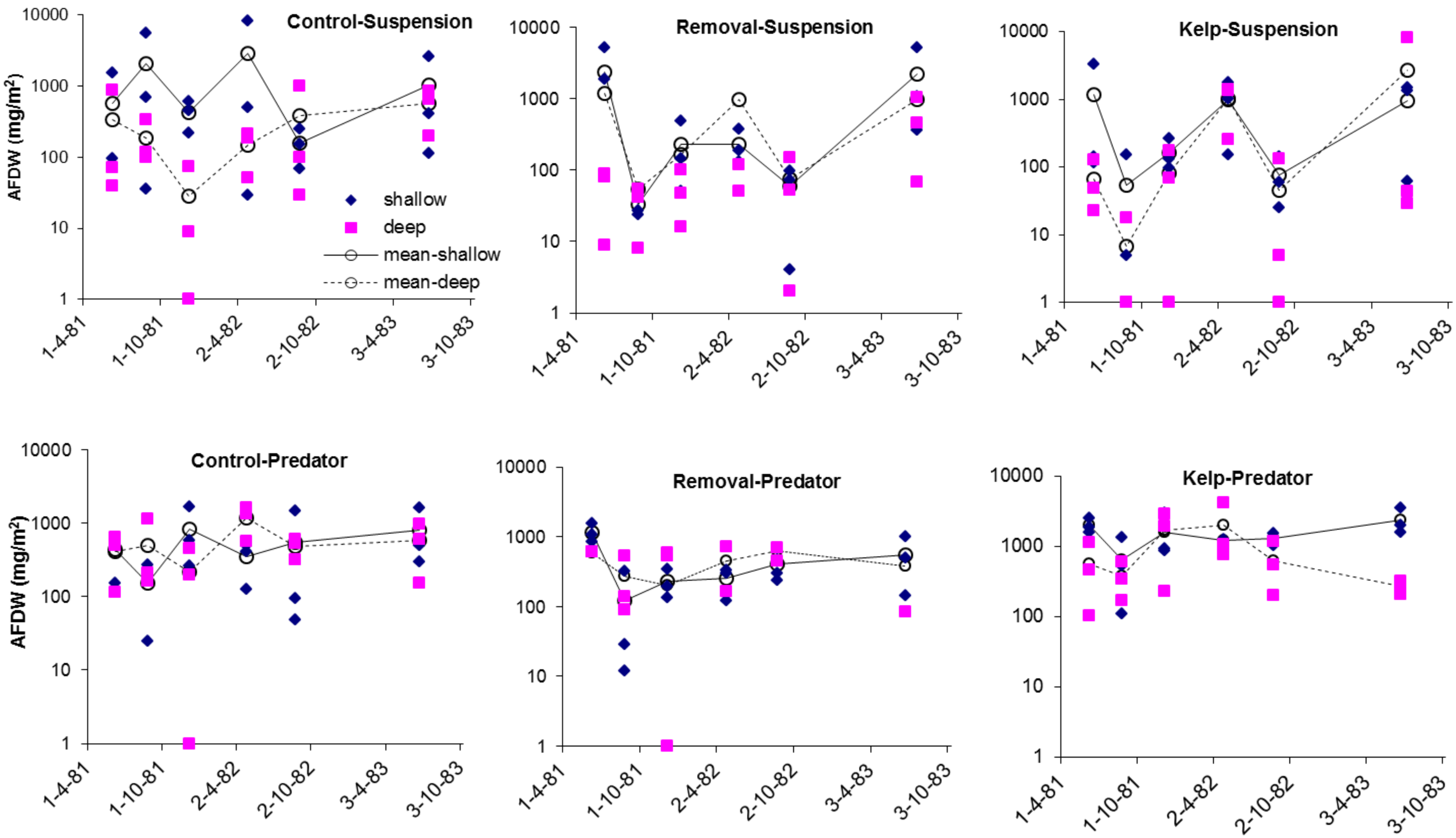


Fig. 12 continued on next page

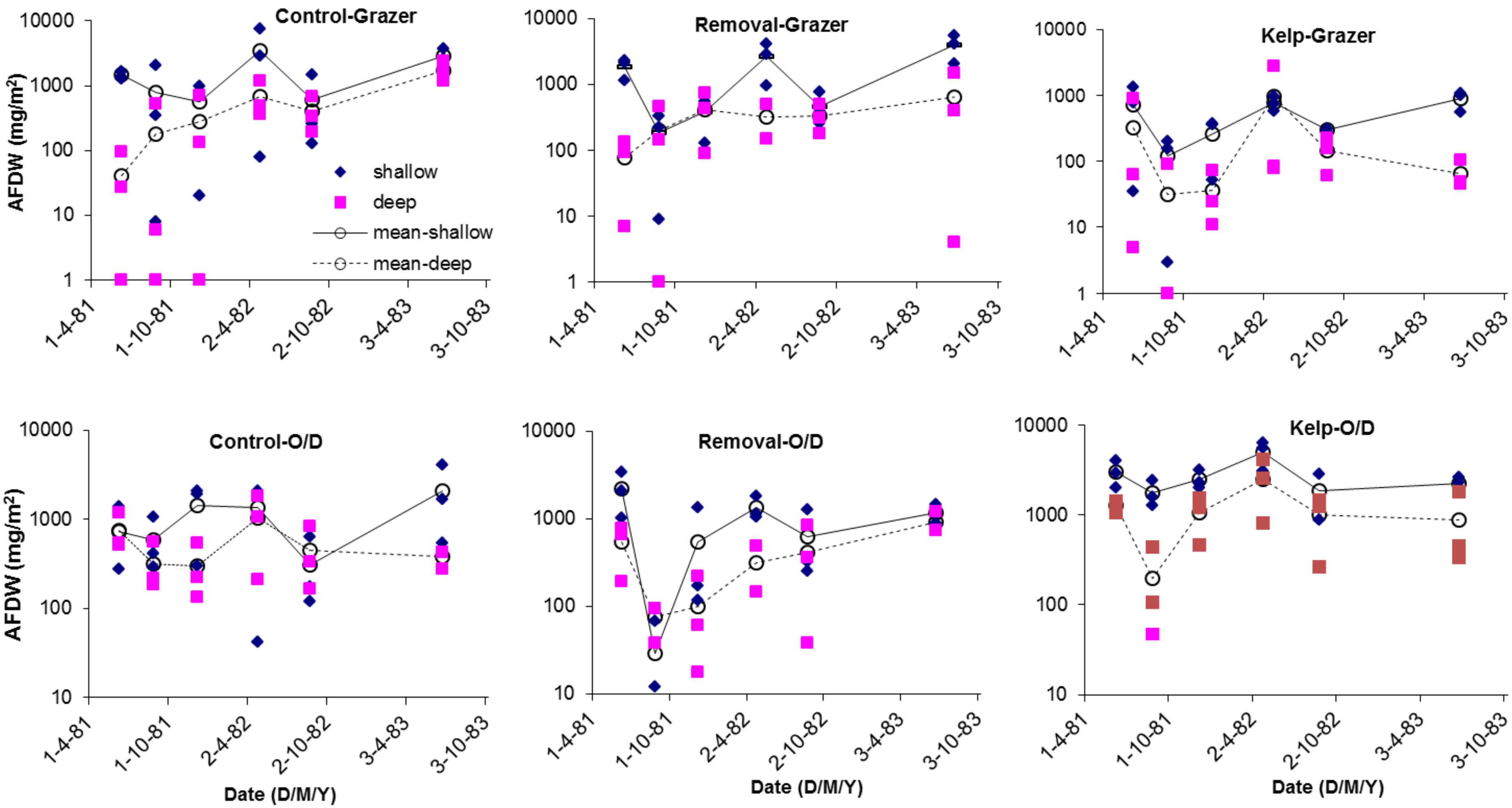


Fig. 12. Biomass (mg AFDW/m^2) of benthos <8 mm in four feeding types collected in shallow and deep halves of the three treatments.

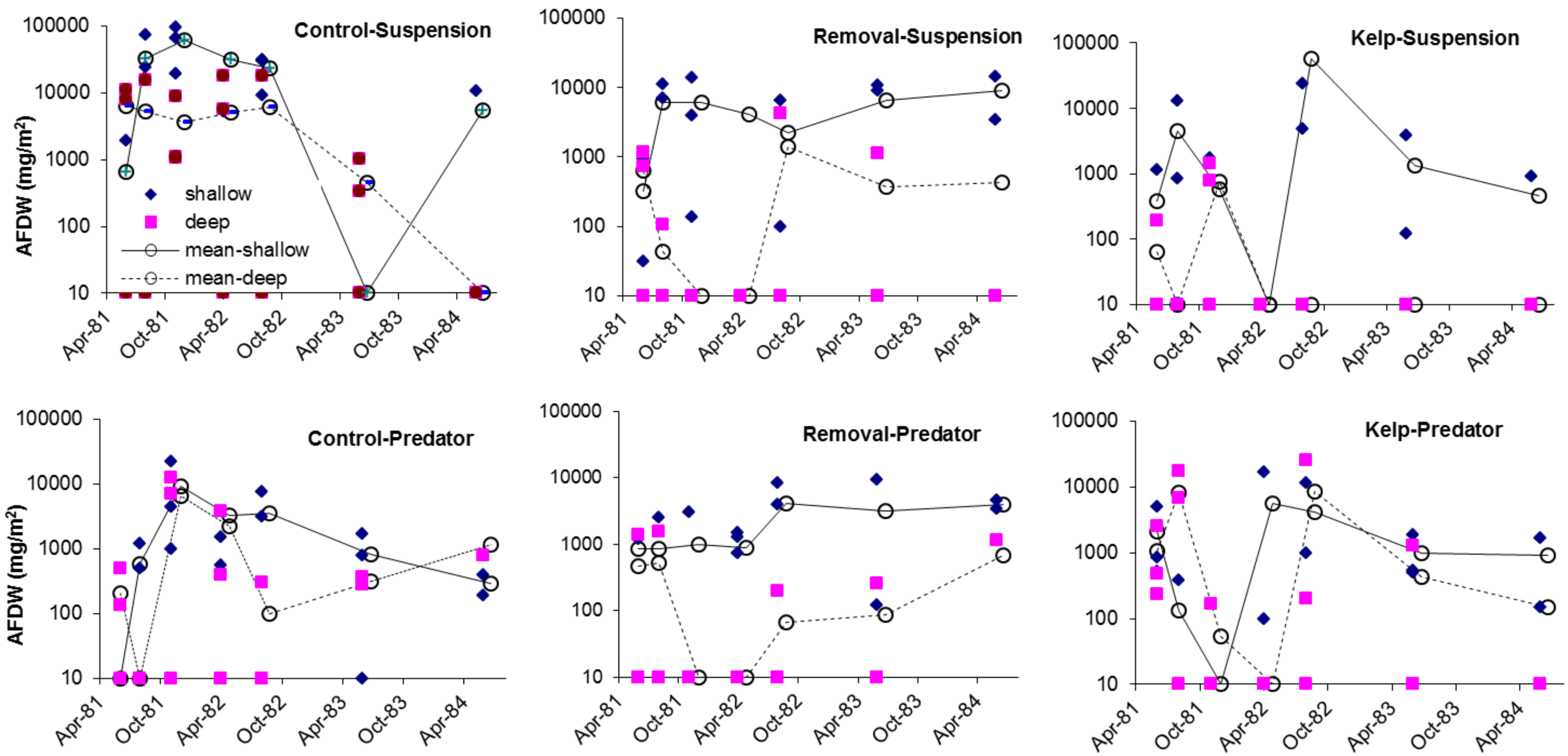


Fig. 13. Biomass (mg AFDW/m^2) of benthos >8 mm in three feeding types found in shallow and deep halves of the three treatments.

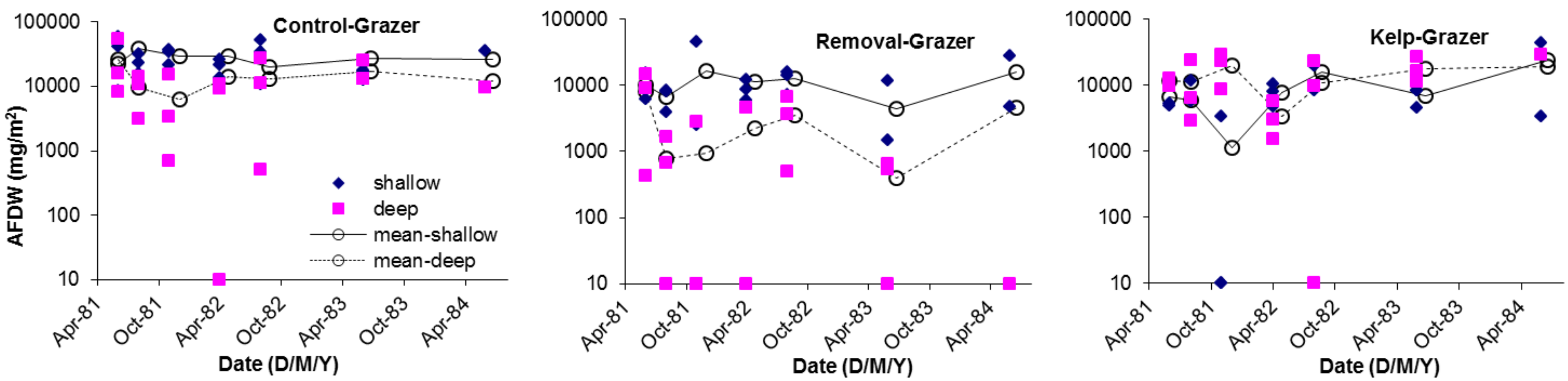


Fig. 13 (cont'd). Biomass (mg AFDW/m^2) of benthos >8 mm in three feeding types found in shallow and deep halves of the three treatments.

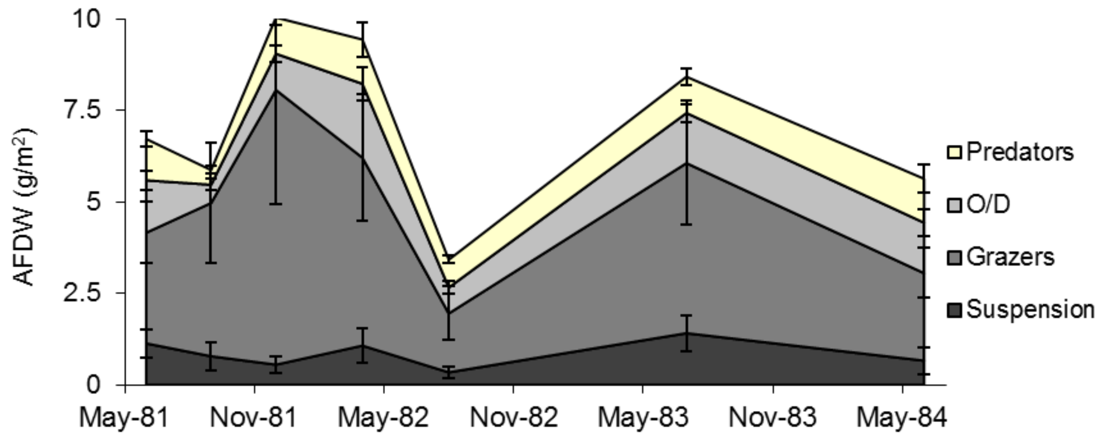


Fig. 14. Benthos biomass (mg AFDW/m^2) by feeding type after summing all sizes <16 mm and averaging over all three treatments. Error bars are +/- one standard error of the mean.

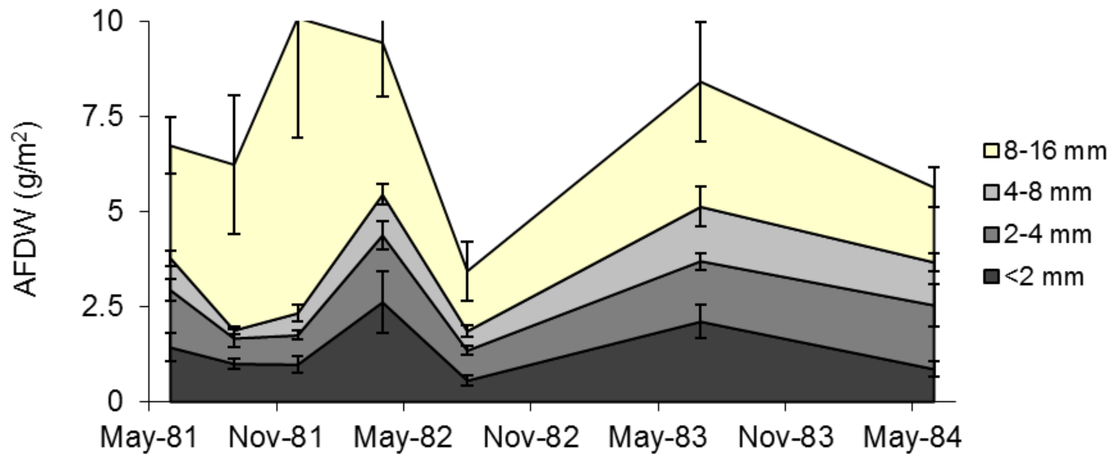


Fig. 15. Benthos biomass (mg AFDW /m^2) by size groups <16 mm after summing over all feeding types and averaging over all three treatments. Error bars are +/- one standard error of the mean.

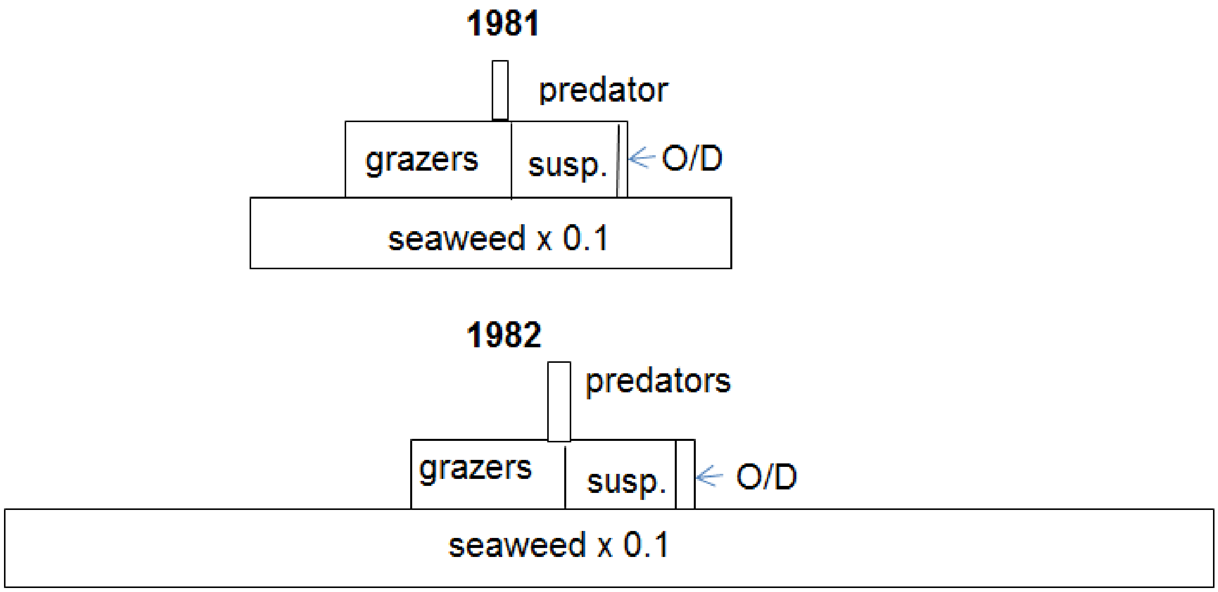


Fig 16. Relative production (g AFDW/m^2) of benthos plus epibenthic plankton for each feeding type for 1981 and 1982. Seaweed production is 10 times the size shown.

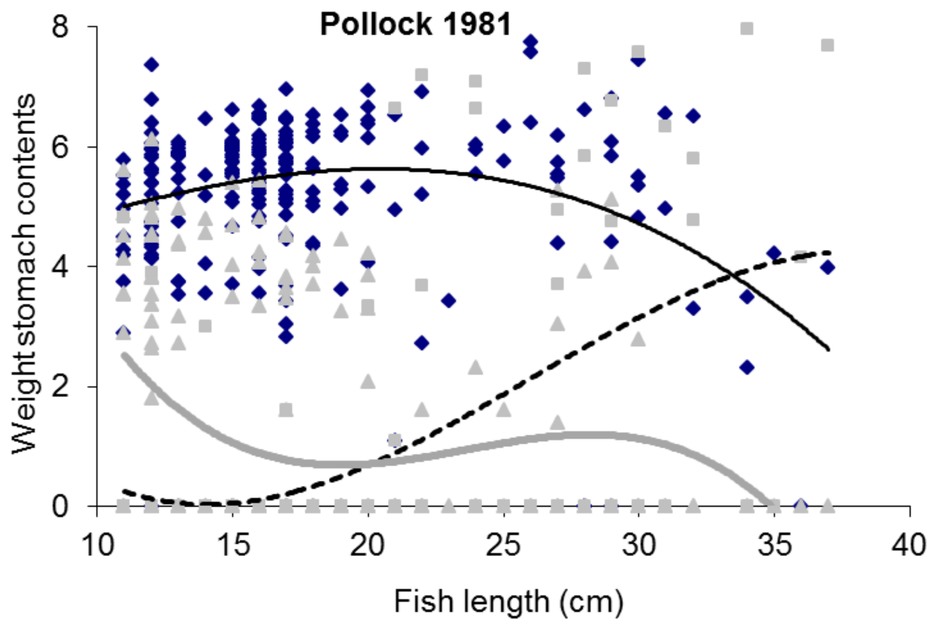


Fig. 17. Weight of pollock stomach contents (ln(mg wet weight +1)) by fish size for fish caught in trammel nets in 1981, three treatments combined. Lines are 3rd order polynomial least-square fits. Solid black line and black diamonds – crustaceans plus polychaetes; dotted line and grey squares – fish; grey line and grey triangles – molluscs.

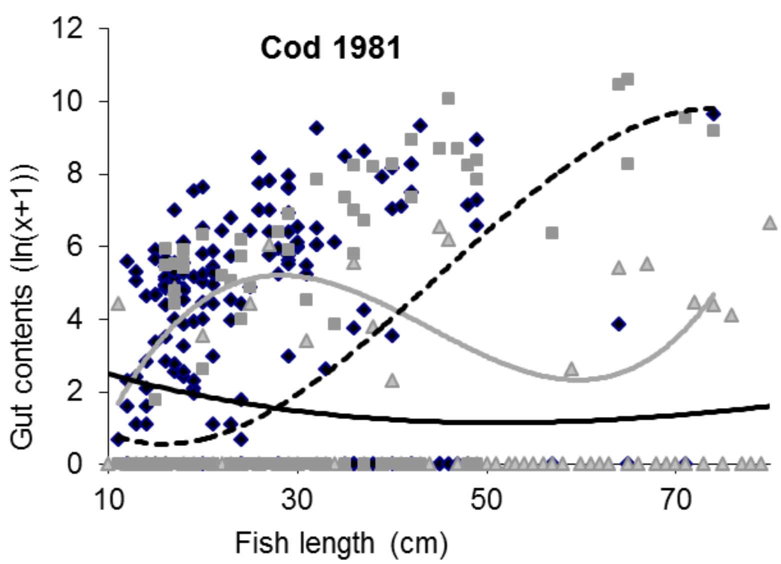
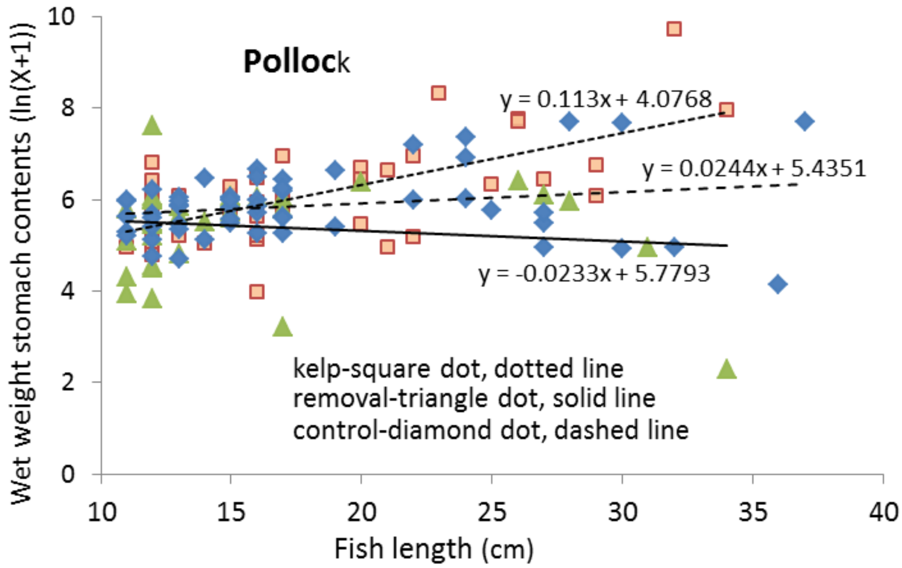


Fig. 18. Weight of cod stomach contents (ln(mg wet weight +1)) by fish size for fish caught in trammel nets in 1981. Lines are 3rd order polynomial least-square fits, three treatments combined. Dotted line and grey squares – crabs; grey line and black diamonds – crustaceans plus polychaetes; solid black line and grey triangles – fish.



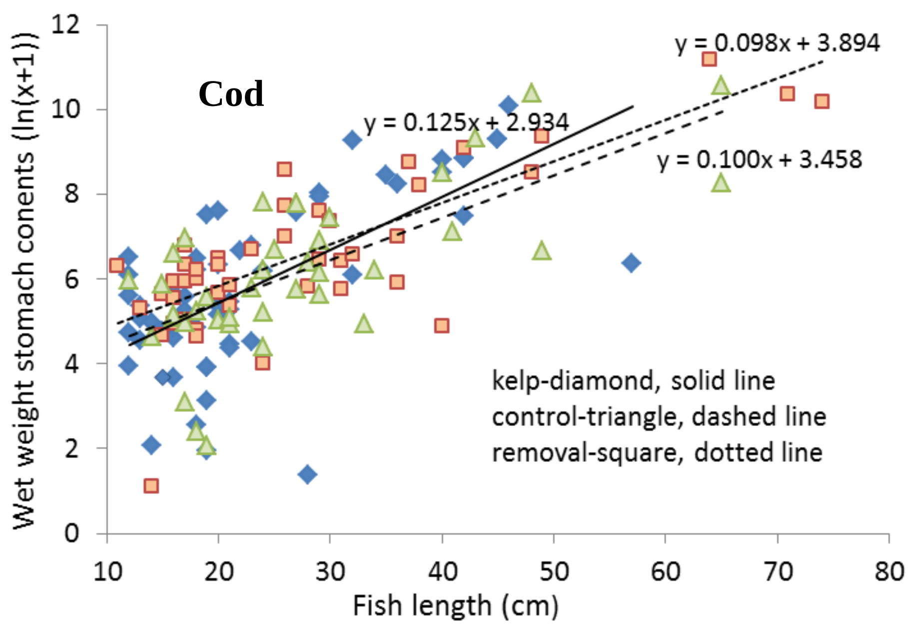
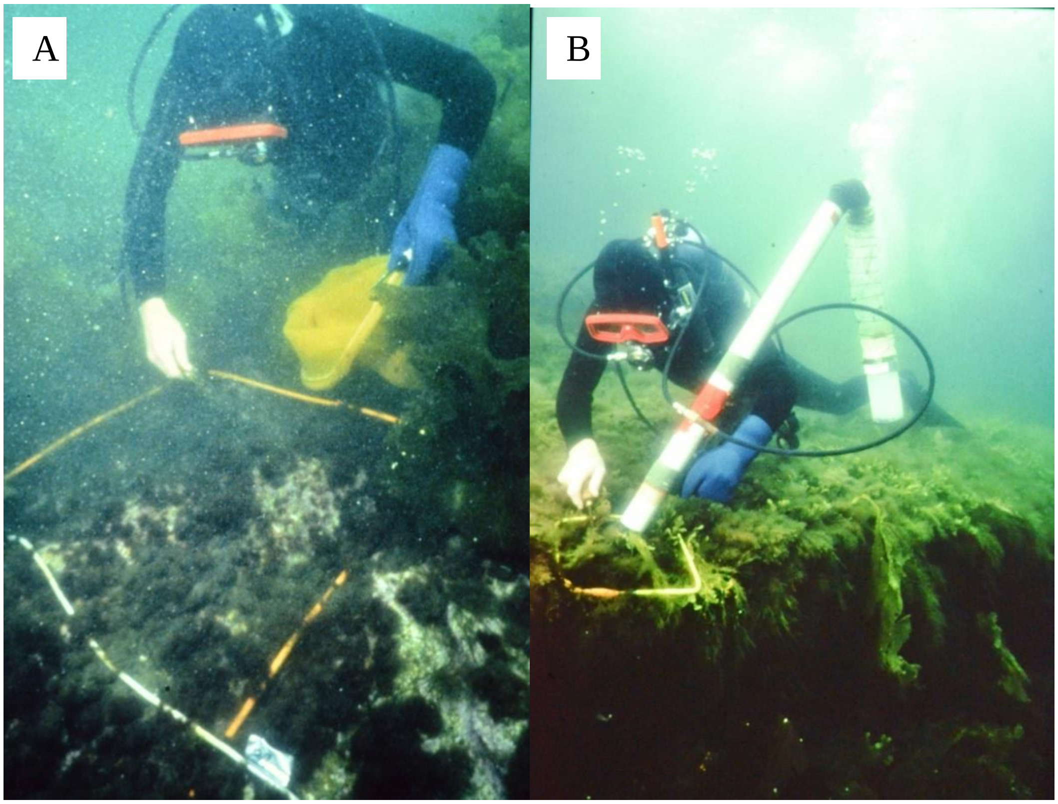
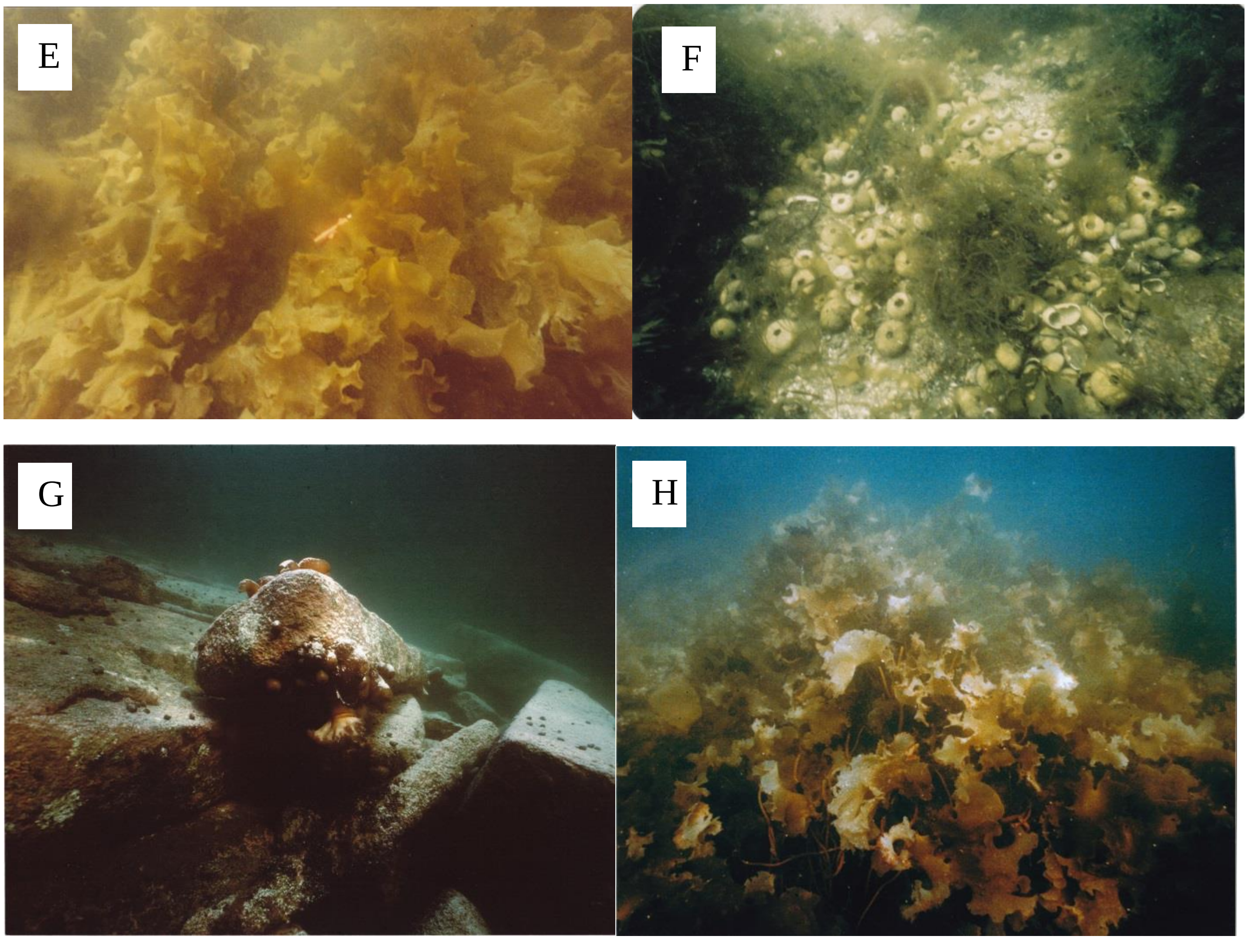


Fig. 19. Weight (ln(mg wet weight+1)) of stomach contents vs. fish length in each of three treatments for pollock and cod. Four sampling periods from June-October 1981 combined. Empty stomachs omitted.

APPENDIX: Photographs of field site



A. Hand sampling from large quadrat.
Transect line at bottom of photo.
B. Air-lift sampling from small quadrat.
C. Trammel net.
D. Irish moss bed in shallow portion of kelp treatment .



E. Large kelp plants (*L. longicruris*) in kelp treatment.
F. Dead sea urchins in control treatment following mass mortalities in September, 1981.
G. Removal area in November 1980 after spreading quicklime.
H. Same location as in G the following July after settlement of *L. longicruris* .