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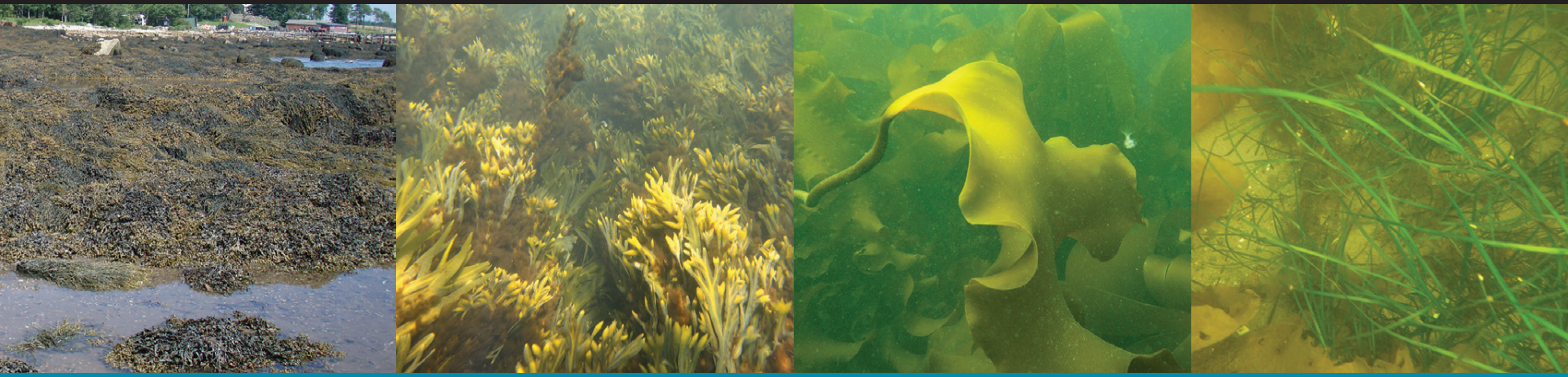

Marine Ecosystem Analysis of Gouldsboro and Dyer Bays, Maine

Walter H. Adey,
Thew S. Suskiewicz, and
Douglas B. Rasher

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ABSTRACT

Adey, Walter H., Thew S. Suskiewicz, and Douglas B. Rasher. Marine Ecosystem Analysis of Gouldsboro and Dyer Bays, Maine. *Smithsonian Contributions to the Marine Sciences*, number 43, viii + 192 pages, 9 figures, 3 tables, 1 appendix (94 appendix figures, 19 appendix tables), 2020. — In the early 1980s, the National Oceanic and Atmospheric Administration (NOAA) initiated an ecosystem analysis of Gouldsboro Bay in eastern Maine as part of a planned marine sanctuary. The original report to NOAA by Walter H. Adey was not published after the sanctuary concept for Maine was abandoned. Because significant human-related climatic and ecosystem changes are underway in the Gulf of Maine, that report provides valuable baseline data and is included as the Appendix to this volume. After qualitatively describing the geological, physical, chemical, and biogeographical features of Gouldsboro Bay and adjacent Dyer Bay, we quantitatively describe the principal bay ecological communities with data collected during the 1981–1983 ecosystem assessment as well as additional measurements taken within the past decade. We then undertake a comparison of the primary productivity of these bays with the Google Earth Pro polygon tool to determine component areas.

Benthic taxa are the dominant primary producers in both bays: rockweeds (primarily *Ascophyllum nodosum*, with *Fucus vesiculosus* secondary) in the intertidal; Irish moss (*Chondrus crispus*, with *Fucus distichus* secondary) as a near monoculture in the lowest intertidal (infralittoral); kelps (primarily *Saccharina latissima*, *Laminaria digitata*, and *Agarum clathratum*) in the rocky subtidal; and the angiosperm *Zostera marina* (seagrass) in soft bottom substrate. The rocky intertidal, dominated by *Ascophyllum* with a specific productivity of 10.6 kg/m^2/year, provides nearly one-third of all bay productivity. Because of the proportionally greater shore length relative to area of Dyer Bay, it has 45% greater productivity for its surface area than Gouldsboro Bay. Kelp has a specific productivity value of 7.2 kg/m^2/year, and *Zostera* of 1.2 kg/m^2/year. The kelps provide approximately 20% of Gouldsboro Bay's primary productivity and 35% of that of Dyer Bay. *Zostera* provides roughly 20% of total primary productivity in Gouldsboro Bay and 12% in Dyer Bay. With a primary productivity of 1.73 kg/m^2/year, salt marshes provide only 3.7% (Gouldsboro) and 2.6% (Dyer) of total primary productivity. With a primary productivity of 0.06 kg/m^2/year, plankton account for 23.8% of Gouldsboro Bay and 16% of Dyer Bay primary productivity.

Cover images (*from left*): *Ascophyllum*-rich rocky intertidal at low tide. Underwater *Ascophyllum* bed at high tide—dark brown filaments are *Polysiphonia lanosa*, a red alga epiphytic on *Ascophyllum*. Underwater kelp *Saccharina latissima* v. *longicruris*. *Zostera marina* at the boundary of the same kelp bed. All photos were taken along western shore of Dyer Bay. Far left photo by Karen Loveland Adey, taken at central western shore; all others by Alex Miller, taken near mouth of bay.

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Marine Ecosystem Analysis of Gouldsboro and Dyer Bays, Maine

Walter H. Adey,[1] Thew S. Suskiewicz,[2] and Douglas B. Rasher[2]

INTRODUCTION

Coastal environments and the ecosystem services they provide are areas of great scientific interest. Changes in these ecosystems, whether driven by localized disturbance or global climate change, can result in reduced ecosystem functions and services. In the Gulf of Maine (GOM), a long history of resource extraction (e.g., fishing), coupled more recently with seawater warming and acidification, has coincided with several large shifts in flora and fauna. Ideally, patterns and drivers of recent ecosystem change can be inferred by comparing historical baseline data to contemporary data. However, in the marine environment, especially in remote areas such as the northern GOM, these ecosystem-based analyses are relatively rare. Such studies are needed as a baseline to gauge future change in the world's oceans.

This study was initiated by author Walter H. Adey (WHA) in 1981 as a marine natural history and systems analysis of Gouldsboro Bay and carried out as a preliminary analysis preparatory to the establishment of a Maine coast national marine sanctuary. The original research, supported by National Oceanic and Atmospheric Administration (NOAA), was canceled mid-project when the concept of a marine sanctuary was abandoned. A final report (Adey, 1982) for the two-year project was written by WHA for NOAA in late 1982 and is published here, for the first time, in the Appendix. Several master's theses, part of a doctoral thesis (Shipp, 1989), and a single publication on the geomorphology of Gouldsboro Bay (Shipp et al., 1985) were completed in subsequent years; the essential elements of those publications have been included in this published version of the report by WHA. Most of the NOAA-supported research remains unpublished and, as an undigitized report, remains unavailable to most researchers. The subjects of this volume, Gouldsboro and Dyer Bays, are located at approximately 44°27′N latitude and 67°56′W longitude, 22 km ENE of Bar Harbor, Maine (Figure 1—see red X on map). Table 1 presents the physical parameters of each bay.

In the 60 years since WHA started his research on the Maine coast, the ecology of the nearshore ecosystem has changed substantially. Once abundant groundfish stocks, particularly cod and haddock, have been depleted (Jackson et al., 2001). Populations of lobsters, crabs, and urchins exploded in the latter half of the twentieth century (Steneck et al., 2013), aided by increased food availability in the form of trap bait (Grabowski et al., 2010) and potentially as an ecological response to the absence of large finfish predators (i.e., a release from predation). After intense fishing in the 1980s and 1990s (Berkes et al., 2006; Johnson

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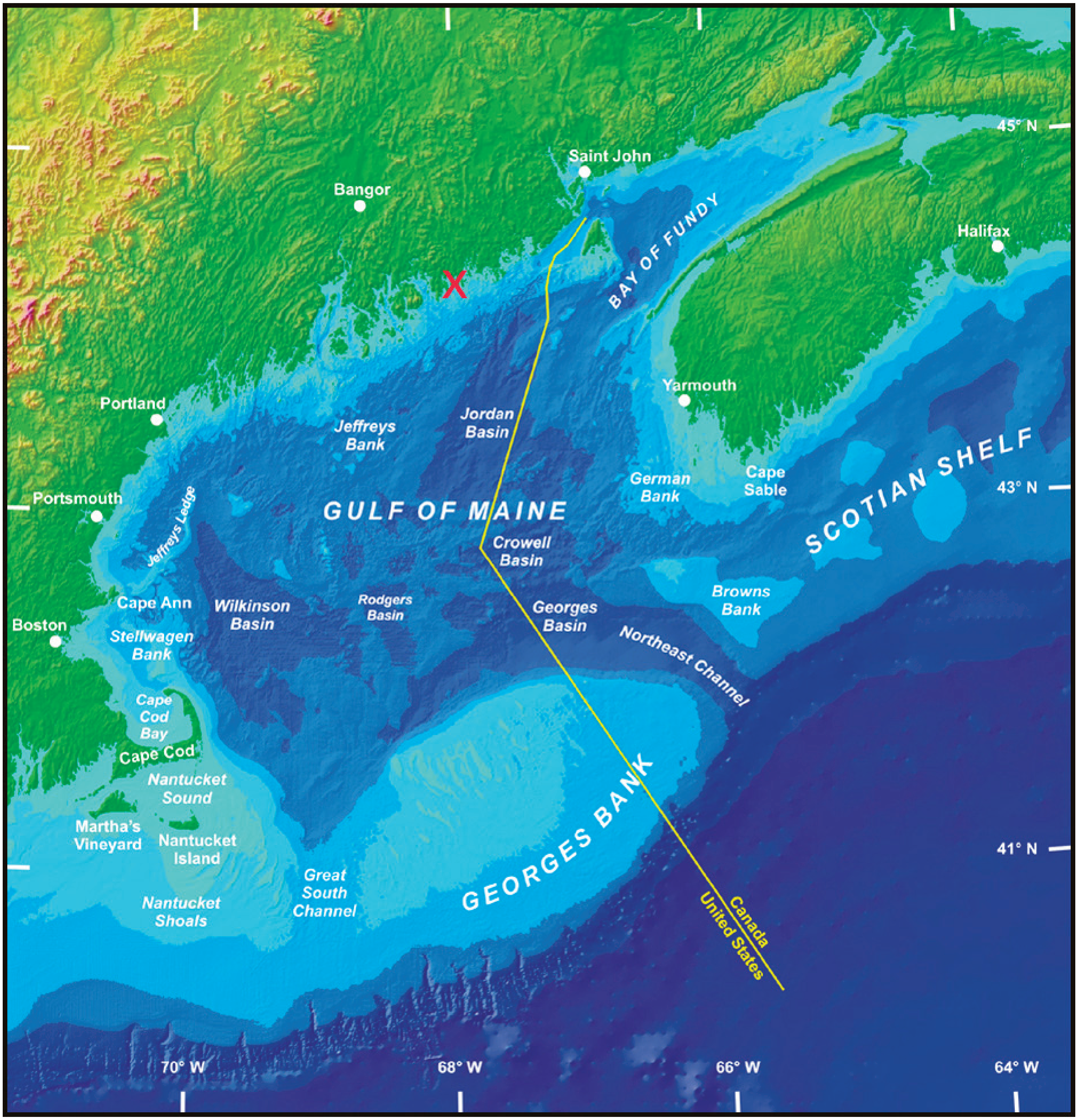

FIGURE 1. Map of the Gulf of Maine with location of the Gouldsboro–Dyer Bay complex indicated (red **X**). The off-lying banks were created as glacial terminal moraines, leaving a complex of basins and ridges that form the Gulf of Maine. Note the St. John (New Brunswick, Canada) label is displaced to the west by about 50 statute miles. Adapted from "Gulf of Maine 2" (https://commons.wikimedia.org/wiki/File:GulfofMaine2.jpg), Canadaolympic989 / CC-BY 3.0, Wikimedia Commons.

TABLE 1. Surface area, hydrology, and marine communities of Gouldsboro (G) and Dyer (D) Bays. Abbreviations: mhwsp = mean high water spring tide; mlwsp = mean low water spring tide. Values in square brackets are sums or percentages calculated for the full group; a dash (—) indicates no data available.

Measured characteristic	**Gouldsboro Bay**		**Dyer Bay**		**Dyer/Gouldsboro ratio**	
Physical characteristics						
Length (centerline)	13,140 m		8,500 m		0.65	
Total shoreline	63,262 m		47,578 m		0.75	
Area (mhwsp)	28,259,791 m^2		11,918,906 m^2		0.42	
Hydrologic characteristics (spring tides)						
Volume (m^3)						
High tide	2.27×10^8		0.80×10^8		0.35	
Low tide	1.61×10^8		0.42×10^8		0.26	
Tidal exchange (m^3)	0.66×10^8		0.38×10^8		0.58	
Tidal exchange (%)	29%		48%		1.66	
Biological communities (area)						
	(m^2)	**%**	**(m^2)**	**%**	**D/G %**	**=f(area)**[a]
Benthic						
Intertidal [Total][b]	[6,694,916]	[23.7]	[2,910,541]	[24.4]	[0.44]	[1.03]
Rocky shore (*Ascophyllum)*	755,710	2.7	491,295	4.1	0.64	1.5
Rocky (miscellaneous)[c]	1,067,844	3.8	701,193	5.9	0.65	1.6
Mud and sand	4,010,253	14.2	1,368,512	11.5	0.34	0.81
Salt marshes (*Spartina*)	699,564	2.5	294,350	2.4	0.41	0.96
Mussel beds (*Mytilus*)	161,545	0.6	55,191	0.6	0.34	1
Subtidal photic: Kelp and *Zostera* beds [Total][b]	[2,602,717]	[9.2]	[1,686,117]	[14]	[0.64]	[1.52]
1/2 kelp; 1/4 *Zostera*	784,209	2.8	1,129,487	9.5	1.45	3.39
1/4 kelp; 1/2 *Zostera*	898,384	3.2	490,126	4.1	0.54	1.28
1/8 kelp; 1/2 *Zostera*	759,097	2.7	66,504	0.6	0.09	0.22
Only *Zostera*	161,027	0.6	0	0	n/a	n/a
Lobster pounds	0	0	75,000	0.6	n/a	n/a
Armored and shell hash	3,000,917	10.6	703,642	5.9	0.23	0.56
Subphotic silt/mud bottoms	15,961,241	56.5	6,544,006	54.9	0.41	0.97
Planktonic (whole bay, mlwsp intertidal)	21,565,875 m^2	76.4	9,008,365 m^2	75.6	0.42	—

[a] The function f(area) indicates the ratio between Dyer Bay and Gouldsboro Bay in proportion to bay area.

[b] Totals for all subcategories.

[c] Includes sand, gravel, black zone, mussel zone, barnacle patches, and isolated rocks with rockweed.

et al., 2013), green sea urchins, the primary subtidal benthic herbivore, became functionally absent from much of the Maine coast. In the intertidal zone, blue mussel populations have decreased by more than 60%, likely resulting from a reduction in propagule settlement (Petraitis and Dudgeon, 2015). Rockweed harvesting is now one of the fastest growing fisheries. The harvest of clams and worms on the tidal flats was once a major supporter of local human populations in the mid-twentieth century; however, in part because of pollution of the upper bays, that fishery is now severely reduced. Moreover, seawater temperatures are now rising, and climate change joins other anthropogenic stressors in these highly impacted bay systems.

The Gouldsboro Bay analysis of the 1980s (see Appendix) measured the primary productivity of the key ecological communities of Gouldsboro Bay. Here, utilizing more recent Google Earth Pro satellite imaging with increased spatial resolution, we recalculate total primary productivity for each benthic habitat and compare the different communities between these contrasting bays. Primary productivity values for *Zostera* and planktonic communities are taken from more recent publications (Larsen, 2004; Ruesink et al., 2017). Through this analysis, we demonstrate that benthic primary productivity in these bays—primarily from macroalgae—exceeds that generated by phytoplankton. We postulate further that bay geomorphology and shape, as determined by ancient drainage basins developed on a complex bedrock terrain, followed by extensive glacial deposition, significantly contribute to the differences observed between these two bays.

The original Gouldsboro Bay study, by including an examination of the extensive soft bottom community with its infauna and a brief analysis of secondary productivity, allowed the development of a preliminary systems diagram based in mass flows. We reference that work (see Appendix), but without the resources to carry out an equivalent survey of Dyer Bay, we do not attempt to expand that part of the NOAA-supported study in this paper.

Geological History

Coastal biotic communities are shaped by their physical environments, which are determined in large part by their underlying geology and hydrology. Shipp et al. (1985) described the geomorphological environment of Gouldsboro Bay in detail, and Adey and Loveland (2007) presented a summary (Figure 2).

The bedrock geology of the Gouldsboro–Dyer Bay complex is primarily that of Paleozoic granites. The surface of these hard granites was repeatedly wiped clean by a series of Pleistocene glaciations, several of which reached well out onto the continental shelf and across the area now occupied by the GOM (Denton and Hughes, 1981). The morphology of the granitic surface, resulting from glacial modification of preglacial stream valleys, controls the basic shoreline shape of bays and therefore wave exposure and, in part, tidal characteristics.

About 13,000 years before present (BP), the northwestward-retreating Wisconsinan glaciers left an irregular layer of till, including both ground moraine and more linear recessional moraines, that provides considerable local modification of drainage, shore morphology, and tidal influence (Denny, 1982; Smith, 1982). Because the current coastal area was greatly depressed by the weight of glacial ice, the coastline was well inland of its present location as the ice retreated. Thus, before crustal rebound, the drowned morainal surface was covered by a thin blanket of bluish glacial clay (the Presumpscot formation). Crustal rebound in the interval of 13,000–10,000 years BP brought the coast well below present sea level (to approximately –60 m), and a thin soil zone was developed on top of the Presumpscot clay (Figure 2, top, dark line beneath fine marine sediment). Recent sea level rise (10,000 years BP to the present) related to continued global-scale deglaciation, has brought the sea level to its present position and has subtidally produced a layer of marine sediment on top of the fossil soil zone (Figure 2, top). Sea level rise has also removed glacial and postglacial sediments from the zone of wave action (Figure 2, bottom) and produced the landforms of a drowned coast, with the shoreline complex of glacial till deposition being reworked by waves and currents. The surficial geomorphology of Gouldsboro Bay is treated in detail by Shipp et al. (1985), and sea level rise relative to coastal topography is shown in the Appendix (see Appendix Figures 46, 47).

The two bays, being tributaries in a small pre-Wisconsinan drainage basin (Appendix Figure 47), show a marked difference in sedimentological character because of the random placement of recessional moraines. Dyer Bay harbors a significant depositional basin in the lower bay, and Gouldsboro Bay harbors a minor basin in the upper bay. Although tidal flows in this system have a role in sediment movement and biological community structure, they are not strong enough to remove the sedimentary basins created by glacial till deposition.

Physical and Chemical Oceanography

Largely because of the macrotidal environment (Garrett, 1972) and the rapid overturn of Maine bay waters, along with a lack of large influent rivers, the GOM, with its distinctive oceanography, has strong control over most coastal bays. In brief, as a result of the shallow terminal moraines of Georges and Browns Banks, the Gulf is a semi-enclosed body of water. Prevailing westerly winds, especially the very strong winter northwest winds, blow surface waters out of the Gulf across the Banks (Figures 1, 3). Over the course of a year, this surface water is replaced by relatively warm (8°–10°C), deep, nutrient-rich, and salty shelf water that enters the GOM through the deep Northeast Channel and by the inflow of fresher coastal water (ultimately largely derived from the Gulf of St. Lawrence) from the Nova Scotia coast. During the winter, the shallow water mass of the Gulf, to 100–200 m deep, is chilled to 1°–5°C, and Coriolis forces form a strong counterclockwise gyre in the Gulf, moving the surface water westward along the Maine coast, and ultimately out of the Gulf over the banks to the southeast (Lynch et al., 1996). Roughly two-thirds of the inflowing water derives from the deep and nutrient-rich slope water coming in through the Northeast Channel, effectively producing an upwelling effect, particularly in the eastern portion of the Gulf (Brooks and Townsend, 1989).

Gouldsboro and Dyer Bays are adjacent to the Eastern Maine Coastal Current (Bigelow, 1927; Graham, 1970; Lynch et al., 1996), a cold current that flows westward from the well-mixed waters at the mouth of the Bay of Fundy. When these bays are flushed by the strong tides, the flushing water is ultimately derived largely from the deep Northeast Channel and its adjacent shelf, as well as the Gulf of St. Lawrence, as previously described. These source waters are largely nutrient rich and prehistorically were responsible for the rich production of eastern Maine bays.

Climate and Biogeography

Gouldsboro and Dyer Bays are mid-latitude coastal indentations on the northeast side of the North American continent. Consequently, on land the atmosphere produces a cold temperate continental climate. In the twentieth century, winter air temperatures often dipped below –10°C at night and most bays froze over during the winter, while daytime summer air temperatures were typically warm, in the 20°–25°C range. On the other hand, as we briefly describe below, the peculiar oceanography of the GOM (Bigelow, 1927; Graham, 1970; Lynch et al., 1996), coupled with a tidal regime driven by the shape of the GOM (Garrett, 1972), provided a water climate that is mixed Subarctic/

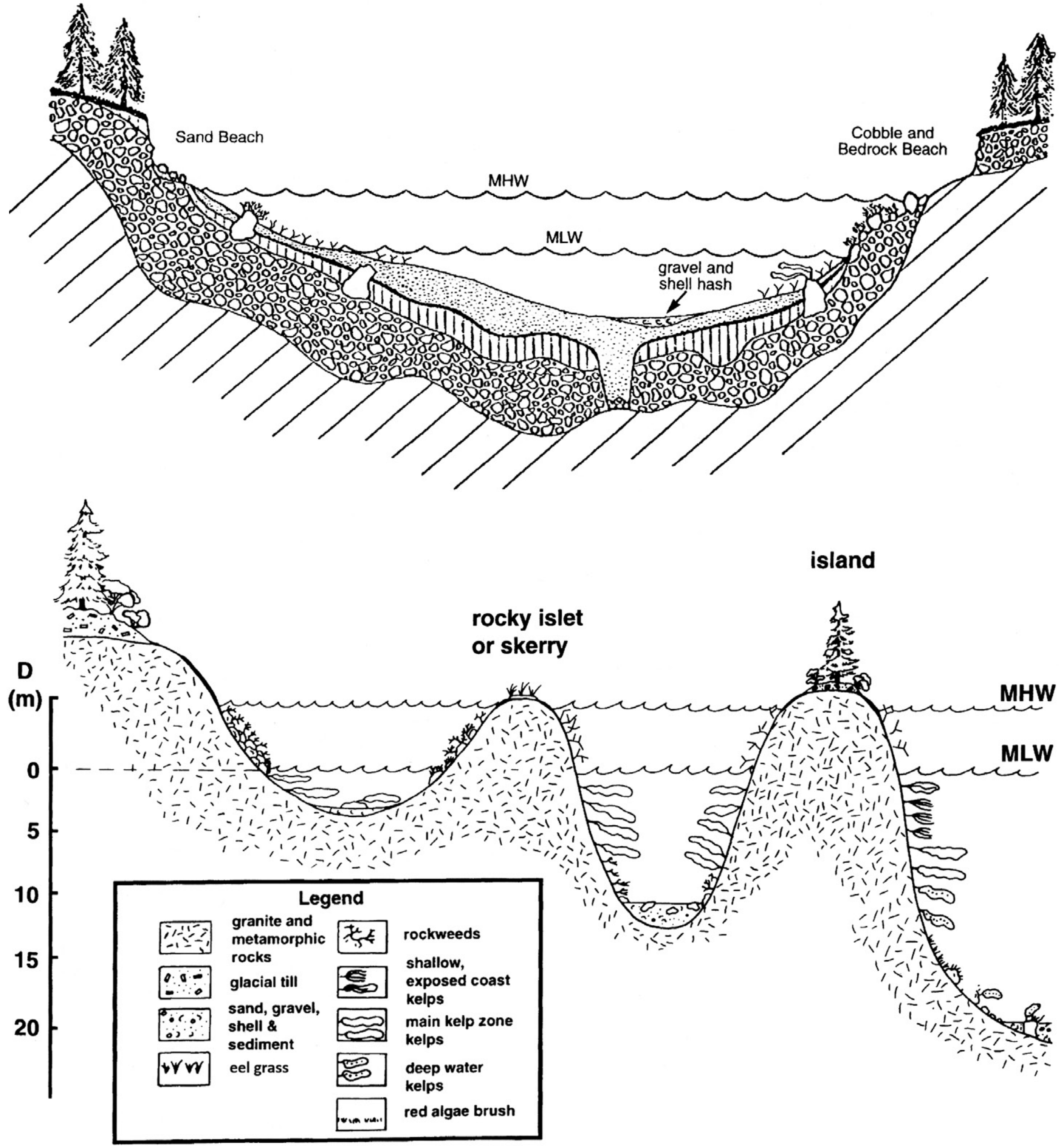

FIGURE 2. Idealized representational cross sections of Gouldsboro–Dyer Bay complex. Top: Upper bay. Bottom: Exposed shore. The geological surface—both bedrock and glacial deposits—as modified by wave action, determines the presence of rocky intertidal and subtidal communities. Abbreviations: MHW = mean high water; MLW = mean low water; D = depth (in meters). The legend for benthic seaweeds and eelgrass in both sections is shown at bottom. Adapted from Adey and Loveland (2007).

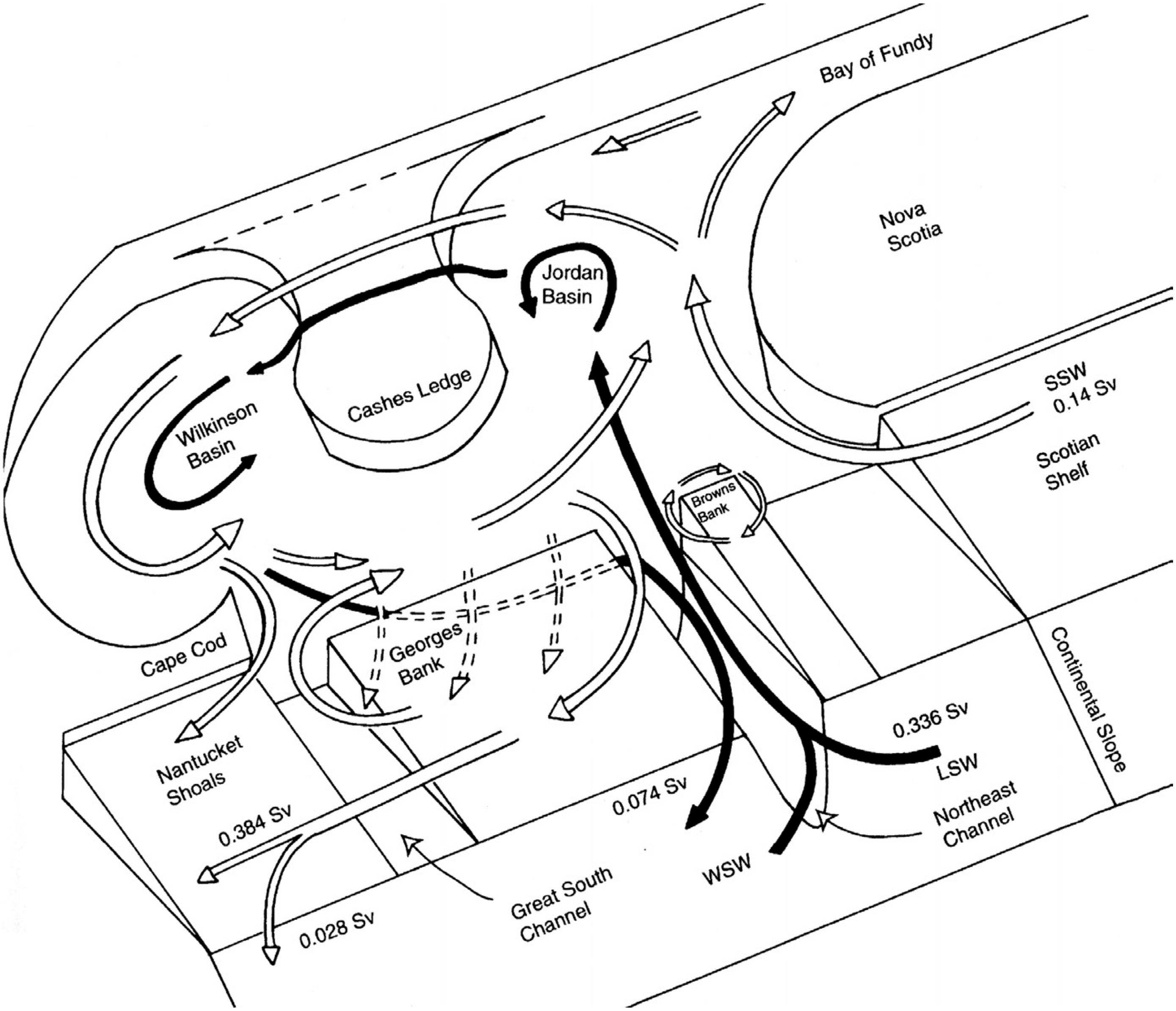

FIGURE 3. Movement of the major water masses in the Gulf of Maine. Diagram shows a counterclockwise arc of flow from the easternmost Northeast Channel to Great South Channel offshore of Cape Cod. The counterclockwise arc runs offshore of the Maine Coast and results in an east-to-west net current along the coast. Legend: dark arrows represent deep water currents; open arrows represent shallow currents; dashed arrows represent winter blow-out water from strong northwesterlies; Sv (Sverdrup) is a unit of flow volume in ocean currents (1 Sv = 1 Mm^3sec^{-1}). Roughly three quarters of the water flow into the Gulf of Maine derives from deep, nutrient-rich, slope water through the Northeast Channel. Most of the remainder is the Nova Scotia coastal current, in part deriving from the Gulf of St. Lawrence and the St. Lawrence River. From Adey and Loveland (2007).

Boreal in the east, toward the mouth of the Bay of Fundy, and cold temperate in the west (Massachusetts Bay), with summer water temperatures in the lower 20°C range.

Shallow benthic communities are significantly controlled by wind-driven wave action. In addition to the cold temperate climate, modified by macrotidal action, the prevailing winds are westerlies, with southwesterlies prevailing in summer and northwesterlies in winter. Although winter winds are offshore on the eastern Maine Coast, the summer southwesterlies provide moderate wave action to the outer coast, thereby providing a rocky shore largely devoid of fine sediment. In addition, storm tracks across the North American continent tend to converge on or just offshore of the GOM. These storms provide northeasterly storm winds, sometimes of great strength, that are considerable modifiers of coastal glacial sediment.

Utilizing the biomass of macroalgal species, the relationship of the algal community structure of the Maine coast to the larger biogeographical framework of the North Atlantic and Holarctic has been described by Adey and Hayek (2005, 2011). The rocky Maine coast is highly dominated by "European" Boreal species in shallow water. However, along the exposed coast, including the outermost parts of the Gouldsboro–Dyer Bay complex, Subarctic species dominate at depths below 5–10 m. During the twentieth century, there has been a considerable summer temperature gradient along the Maine coast with colder temperatures (~10°C) in the east and warmer temperatures (~20°C) in the west (Garrett et al., 1978; Lynch et al., 1996). As Adey and Steneck (2001) have shown, based on the abundance of coralline algal species in mid-century, the easternmost Maine coast biogeographically laid close to the North Atlantic Subarctic core (the Strait of Belle Isle between Newfoundland and Labrador), whereas the westernmost Coast (Massachusetts Bay) was almost entirely Boreal in character, and the outer Nova Scotia Coast to the east, dominantly Boreal, had a lower percentage of Subarctic species in deeper water. The GOM has recently entered a period of rapid warming, which may have corresponding effects on the biota and the functioning of these bay ecosystems.

Larsen (2004) proposed a "uniquely" high biodiversity for Cobscook Bay within the western North Atlantic and related that high biodiversity to the large tides of that bay. However, "exceptional character" referred to a contrast with the generally well-studied central Maine coast and the western GOM where Subarctic species (adding to the dominant Boreal flora) were less abundant or absent. An understanding of the biogeographical development of the marine coastal Northern Hemisphere, as well as the evolution of the macrotides related to the shape of the Bay of Fundy, is also essential to understanding that "unique" biodiversity. It is not just Cobscook Bay, but the eastern GOM in general, that has provided the conditions for local high biodiversity based in the mixing of Boreal and Subarctic species over a vertical and offshore/inshore gradient. The location of the Gouldsboro–Dyer Bay complex within that framework is important.

The purpose of this paper is to examine the ecosystem characteristics of two typical bays on the eastern Maine Coast, especially regarding community structure and primary productivity. Our primary interest is in the principal physical/geological controlling factors, the extent of ecological communities, their dominant organic components, and the elements of primary productivity. It is not our intention to examine the flora and fauna of these bays in taxonomic detail. Modern taxonomic studies exist that can provide identifications of organisms (e.g., Trott, 2004; Mathieson et al., 2008; Sears, 2002), and numerous research papers exist that cover the biology and ecology of individual species throughout this region (e.g., Bryson et al., 1994; Scheibling and Hatcher, 2001; Petraitis et al., 2008; Kordas and Dudgen, 2009; Johnson et al., 2012; Steneck et al., 2013).

MATERIALS AND METHODS

We assessed the rates and sources of primary productivity of all major community types of Dyer and Gouldsboro Bays and characterized the hydrography and geological history of this region. A detailed description of the materials and methods utilized in the Gouldsboro Bay precedent study in the early 1980s is shown in the Appendix. Briefly, intertidal, subtidal, and planktonic communities were assessed across multiple regions within and outside the bay throughout the year. In each of these areas, researchers quantified the biota periodically during a two-year period, including during the winter months. Both the intertidal and subtidal zones were sampled with 1/16 m^2 quadrats (individual zone sampling, *n*, ranged from 6 to 28) at three different tidal heights (intertidal) and three different depth zones (subtidal). Quadrats were haphazardly placed within each target depth zone (intertidal: 2–3 m, 0.5–1 m, and –1 to 0 m, mean low water; subtidal: 2.5 m, 5 m, and 10 m, mean low water). For each quadrat, all conspicuous macroalgae and invertebrates were assessed, and species-specific biomasses were obtained.

We estimated total primary productivity ($g/m^2/day$) for the dominant intertidal rockweed *Ascophyllum nodosum* utilizing demographic data based in the annual weight increase of growing branch tips in Gouldsboro Bay (see Appendix, p. 23); those data are compared with more recent studies in Cobscook Bay (Vadas et al., 2004a). Kelp growth was measured for the three most common species (*Saccharina latissima*, *Laminaria digitata*, and *Agarum clathratum*) using the hole-punch method (sensu Mann, 1973; also described in the Appendix pp. 29–30), which provides a measurement of total elongation (cm/day) independent of distal tissue loss. *Zostera* (eelgrass) is essentially an annual in these bays, so annual productivity was estimated from late summer standing crop in mudflats and shallow subtidal environments (see Appendix pp. 59–60, Appendix Table 17). In addition, photointensity (and thereby attenuation and turbidity) throughout the bay was recorded during the summer months within 1 h of the solar zenith using a submersible photosynthetically active radiation (PAR) sensor (Li-Cor LI-185A; LiCor Inc.) at depths of 0, 2.5, 5, and 10 m.

Soft bottom habitats were sampled with a series of box cores ($n > 90$). For each core the size fraction and percentage of organic material were determined, and all macroinvertebrate species were recorded. Nutrient data were collected by freezing filtered water samples and returning them to the Marine Systems Laboratory at the Smithsonian Institution for calorimetric analysis. Plankton and zooplankton collections were made by towing nets of 90 μm and 150 μm mesh size from a small boat. Phytoplankton primary productivity was determined by the ^{14}C method using a Packard 2660 liquid scintillation counter. Phytoplankton biomass was examined both as chlorophyll concentration and as ^{14}C uptake in suspended light/dark bottles. These standing crop and productivity data are compared to those available for other bays in the literature, and in some cases, we utilize those results or modify the Gouldsboro results accordingly where the data are more extensive (Vadas et al., 2004a–c). Although most data were collected in Gouldsboro Bay in the 1980s, the authors re-sampled the hard bottom substrate in 2017 and 2018 for the purpose of detecting shifts in the macroalgal and macroinvertebrate communities. Inter-decadal changes in the biota are covered briefly in the Discussion but are the focus of another manuscript.

The intertidal zone of Dyer Bay was surveyed by skiff and on foot during a 2009 summer field season, and numerous still images were taken for future comparison. Twenty-three subtidal cross-shore scuba transects distributed from north to south in Dyer Bay were carried out from mean low water spring tide (mlwsp) to the limit of rock, gravel, or shell substrate. Still images and video footage were taken along the transects, and these data were utilized in determining the extent of subtidal communities. These data are available from the Smithsonian Natural History Museum coralline and algal herbarium (National Museum of Natural History, Botany Department, 2019).

The original community mapping presented in the Appendix was based on National Ocean Service (NOS) nautical chart 13324 and a low tide photomosaic made from 9 × 9 black and white aerial photographs taken on 16 May 1944 by the former Coast and Geodetic Survey (C&GS). In this updated study, we utilized Google Earth Pro photo mosaics (25 September 2016), which were taken near mlwsp on an extremely calm day (e.g., individual lobster floats are visible). The spatial resolution from the Google Earth Pro mosaics was substantially better than the earlier C&GS surveys used in the Appendix; resolution within Google Earth Pro is approximately 65 cm, whereas the C&GS surveys were more (approximately 2–5 m).

The Google Earth Pro polygon tool was used to measure community area in both Gouldsboro and Dyer Bays (Figures 4–6). Finer-scale features such as rocky intertidal, subtidal, and *Mytilus* beds were mapped at an eye height of 185 m (600 ft); larger-scale areas, such as mudflats and salt marshes, were mapped at an eye height of 1,850 m (6,000 ft). Rocky intertidal covered with rockweed was measured first, followed by the entire non-mudflat intertidal. The latter consisted largely of the higher black zone (lichen/cyanobacteria zone), intermittent pebble, gravel, and sand patches, and the lower intertidal/infralittoral *Mytilus edulis*/*Chondrus crispus* band; it was separated from the

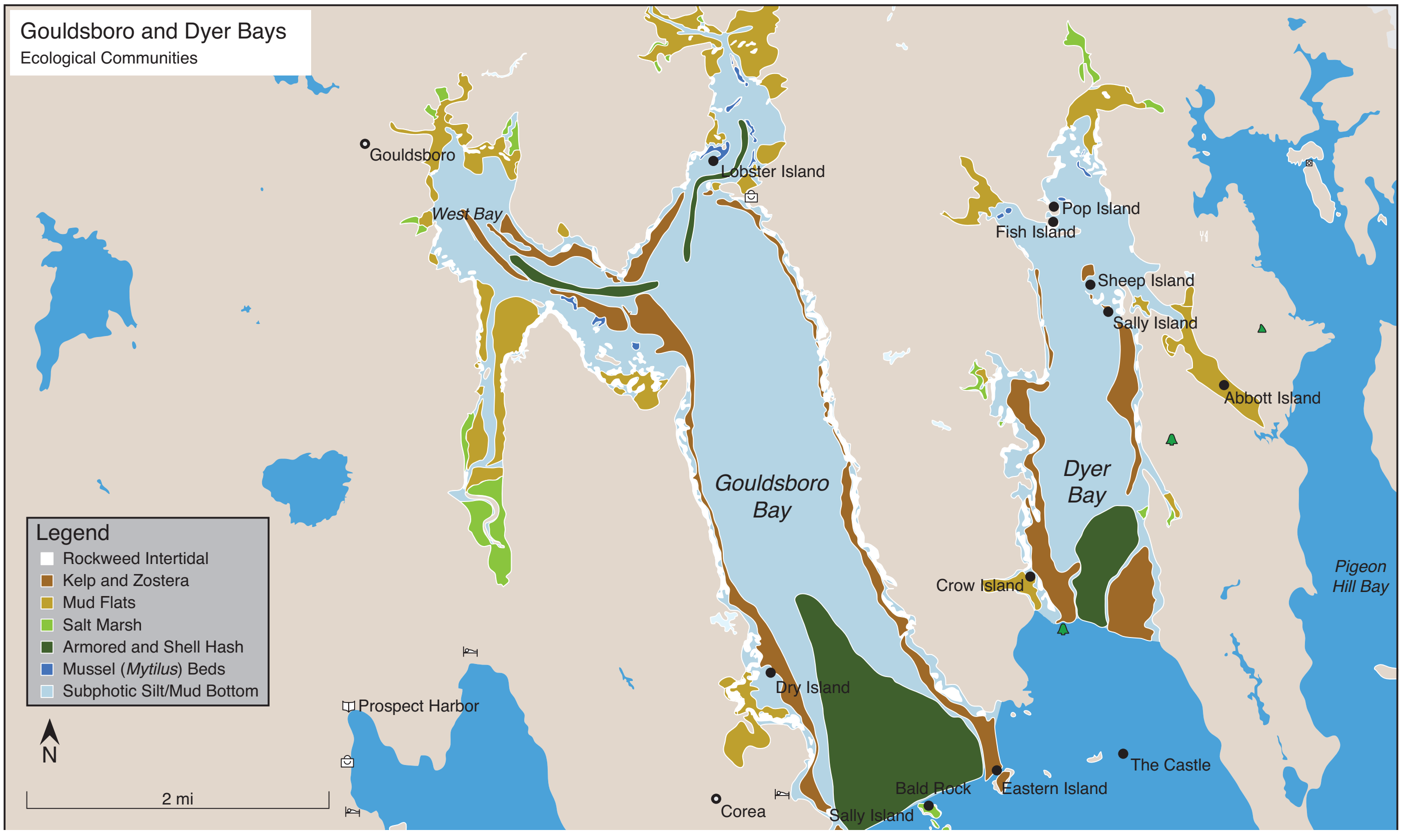

FIGURE 4. Gouldsboro and Dyer Bays at an eye altitude of 13,400 m (43,550 ft). Intertidal community boundaries taken from low-altitude imaging (see Figures 5, 6) as verified by ground truthing. Subtidal community boundaries were verified by diving on transects. Color coding as follows: white-outlined areas, rocky intertidal; brown, kelp (exposed) grading to *Zostera* (protected); gold, mudflats at low tide; light green, salt marsh; dark green, armored bottom/shell hash; dark blue, *Mytilus* mussel beds; light blue, subtidal soft bottom (margins verified by divers); medium blue, unstudied lake and bay areas; beige, land. Map created with and adapted from Google Earth Pro.

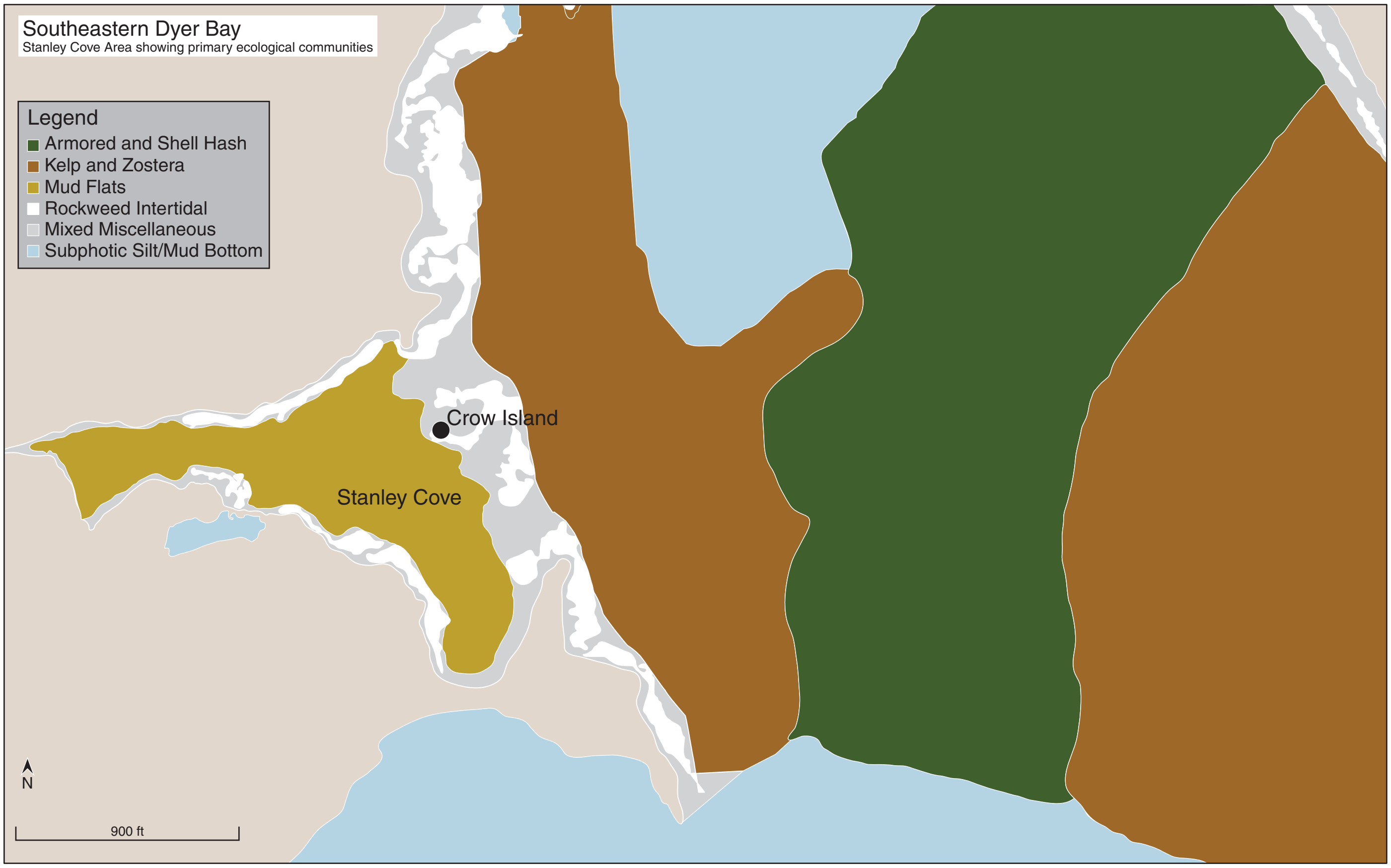

FIGURE 5. Stanley Cove area of southwestern Dyer Bay at an eye altitude of 964 m (3,136 ft), showing the primary ecological communities of the Bay. Additional notes on color-coded areas: dark green, armored bottom/shell hash; brown, kelp (exposed) grading to *Zostera* (protected); gold, mud flats at low tide; white, rockweed intertidal; gray, mixed miscellaneous—these areas between the high tide shoreline and either subtidal mud flat (gold) or the kelp/*Zostera* (brown) zones include both rockweed intertidal (white) and a mixed community of black zone, patchy rockweed, sand, and an infralittoral mussel band with scattered *Chondrus* sp. in more exposed areas (not labeled). Map adapted from Google Earth Pro.

rockweed zones by subtracting the total area from the rockweed zones in units of about 200 m in length. This separation was not accomplished in the earlier study because sufficient detail was lacking in the geographic tools available at that time.

We assume that there has been little change in substrate area between the survey times of the early 1980s (Gouldsboro Bay), in 2009 (Dyer Bay), and the Google Earth Pro images of 2016. Visual comparisons between the original C&GS images and those provided by Google Earth Pro showed no apparent significant shifts in substrate for either bay. Productivity data are derived from the 1980s surveys; the community productivity data presented herein are those of the 1980s and therefore provide the baseline time for future analyses. We treat these issues again in the Discussion.

The physical dimensions and hydrography of Gouldsboro and Dyer Bays were obtained from C&GS Hydrographic Chart 13324. To determine high tide and low tide volumes (based on mhwsp and mlwsp) for each bay, we first divided the entire region into a grid of cells 10 m per side. The average depth for each cell was determined from the chart soundings to obtain high (mhwsp) and low (mlwsp) volumes. From those data, we were able to obtain the amount of bay flushing at spring tides (i.e., the percent change in water volume between high and low tides; see Table 1).

RESULTS

Biomass/Standing Stock of Principal Communities

Community areas for both bays are shown in Table 1, and the standing stocks (biomass) of the principal components of primary productivity are shown in Table 2A–C (modified from the Appendix). Primary productivity was dominantly provided by benthic macrophytes in both Gouldsboro and Dyer Bays; phytoplankton was a minor component of total productivity (see Table 3).

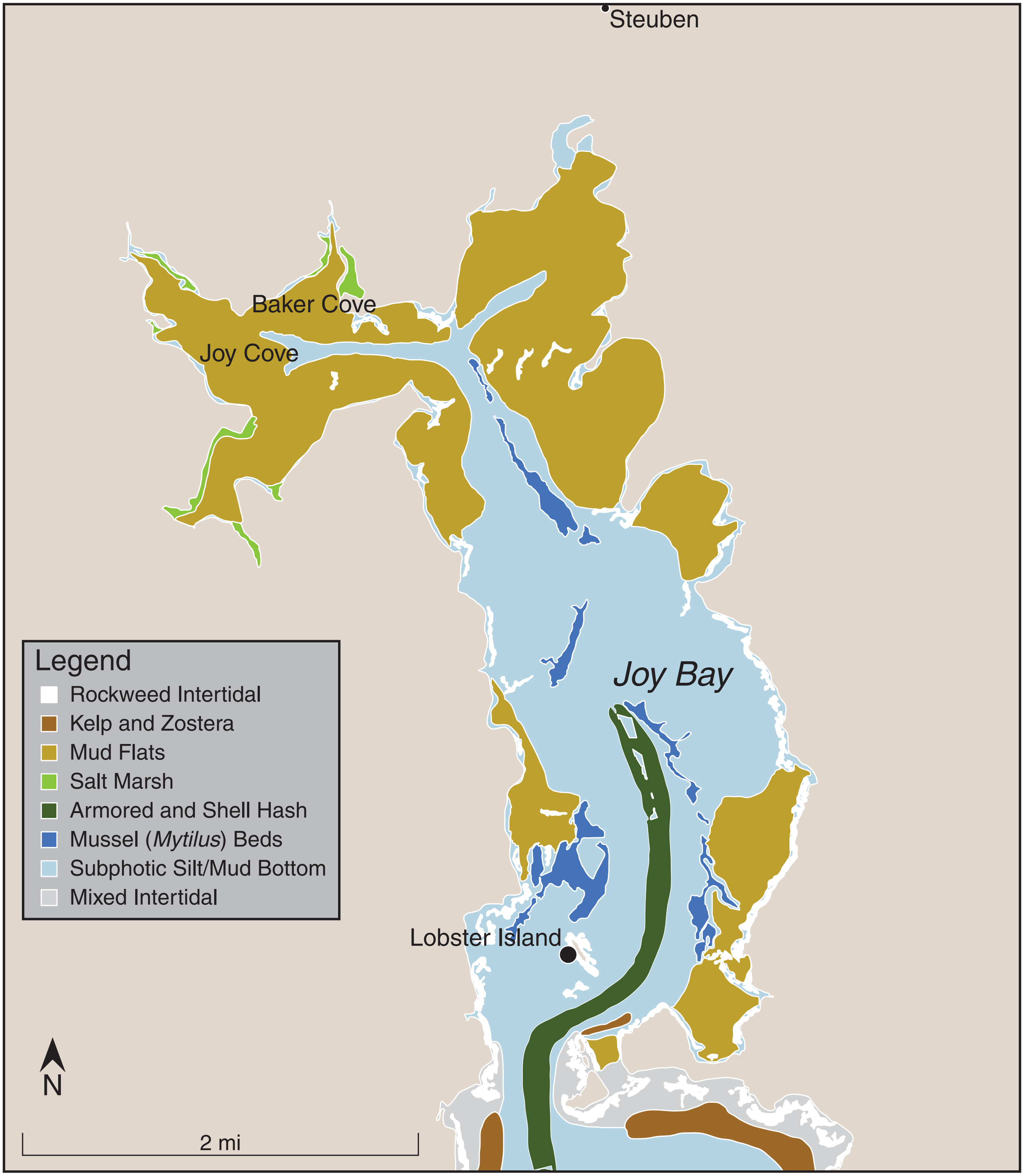

FIGURE 6. Northern Joy Bay region of Gouldsboro Bay at an eye altitude of 3,158 m (10,262 ft), showing the bay's primary ecological communities. The mixed intertidal community designation and other notes on color-coded areas are as described in Figure 5 caption. Note the abundance of *Mytilus* beds (dark blue), a characteristic of both Gouldsboro and Dyer Bays in the northernmost mudflat regions. Map adapted from Google Earth Pro.

The dominant primary producer communities in Gouldsboro and Dyer Bays included rockweeds (primarily *Ascophyllum nodosum* with *Fucus vesiculosus* secondary) in the intertidal; Irish moss (*Chondrus crispus*), which often forms a near monoculture under the rockweed in the lowest intertidal (the infralittoral zone between spring and neap tides, with *Fucus distichus* secondary in exposed areas); the kelps (primarily *Saccharina latissima*, *Laminaria digitata*, and *Agarum clathratum*) in the rocky subtidal; and the angiosperm *Zostera marina* (eelgrass) in soft bottom substrate (Table 2). These results are largely consistent with the extensive studies of Vadas et al. (2004a–c) for Cobscook Bay and those by Adey and Hayek (2011) for the entire Maine coast.

The Gouldsboro Bay study in the 1980s (Appendix) analyzed the planktonic community, the range and effects of the principal macroinvertebrate grazers and predators, and the soft bottom infaunal community. Other than carrying out visual surveys, as described above, we have not had the resources to carry out equivalent studies on Dyer Bay. However, as indicated from these manual surveys, as well as the still images and video footage, the larger-scale community structure and standing stock are similar for these two bays. Some conspicuous changes in more recent surveys include an abundance of green crabs and barnacles in 2009 in the rocky subtidal and a greatly reduced number of sea urchins. In the Discussion, we consider the potential role of the overharvest of sea urchins in the 1980s to 1990s in changes to subtidal kelp biomass. The biomass of the green urchin *Strongylocentrotus droebachiensis* in 1981–1982 frequently exceeded 500 g/m^2 throughout Gouldsboro Bay (see Appendix Table 8), and sea urchins were the dominant mobile invertebrate (Johnson et al., 2013). It appears that urchin density has decreased by at least two orders of magnitude in the lower bay and along the exposed shoreline of both bays. Sea urchin standing stocks presented in the Appendix are those of 1982, preceding sea urchin reduction resulting from extensive harvesting effort.

PRIMARY PRODUCTIVITY

Analyses were carried out in summer, except for the kelps, which were studied in both summer and winter. The summed primary productivity results for both Gouldsboro and Dyer Bays are given in Table 3, with a comparative analysis of the two bays.

Macroalgae: Intertidal

The *Ascophyllum* rocky intertidal provided a specific productivity of 10.6 kg/m^2/year (Appendix). Because the intertidal of these bays tends to occur as more or less large rock "reefs" that could be separated in the Google Earth images, these were measured as a unit and then the entire (generally rocky) intertidal was separated as a miscellaneous zone (upper black zone and *Spartina* patches, scattered boulders with *Ascophyllum*, lower *Mytilus* zone, barnacle patches, and sand and gravel areas). This zone has more scattered algae, including patches of *Ascophyllum*, *Fucus*, and *Chondrus* (lowest intertidal), as well as the photosynthetic Cyanobacteria of the black zone, and thus provides significant primary productivity. We estimated the productivity of the miscellaneous zone as one-quarter of those areas more dense in *Ascophyllum* (see Table 2B for the infralittoral) and assigned a value of 2.1 kg/m^2/year. As can be seen from Table 3, the rocky intertidal provides about one-third of productivity of both bays (with the *Ascophyllum* "patches" comprising one-quarter of the total). The rocky intertidal of Dyer Bay provides more than 60% productivity of the total (as compared to Gouldsboro Bay). In Dyer Bay, the proportion is higher because of bay size and shape and the proportionally greater amount of rocky shore (Table 1).

Macroalgae and Zostera: Subtidal

The current study is restricted to the bays (see Topography, below), where more exposed rocky bottoms tend to include sandy-mud patches, which are usually occupied by *Zostera*. A gradual but irregular change occurs in this zone, from all kelp at the bay mouths to all *Zostera* at the upper bay reaches. Pure kelp quadrats have a specific productivity value of 7.2 kg/m^2/year and pure *Zostera* quadrats are 1.2 kg/m^2/year (see Appendix) (Ruesink et al., 2017). Based on those values, we have developed an exposure gradient, ranging from exposed to protected (kelp: *Zostera*) in our analysis (Table 3). The kelps provide approximately 20% of the Gouldsboro Bay primary productivity and 35% of that of Dyer Bay; as in the intertidal, the relatively longer Dyer Bay rocky shore provides for a substantially greater proportion of whole bay productivity.

Zostera (eelgrass) is essentially an annual in these bays (see Appendix), so annual productivity has been estimated from late summer standing crop on mudflats and in the shallow subtidal environments. With a specific productivity of 1.2 kg/m^2/year both on intertidal mudflats and subtidally, *Zostera* provides roughly 20% of total primary productivity in Gouldsboro Bay and 12% in the adjacent Dyer Bay (Table 3). The productivity proportion of Gouldsboro Bay is higher than that of Dyer Bay largely because of the greater extent of *Zostera*-covered mudflats in Gouldsboro Bay.

Salt Marsh

Salt marsh primary productivity at 1.73 kg/m^2/year is derived from the literature (Roman et al., 1990). This latter study, on the large Nauset Marsh on Cape Cod, is a whole marsh analysis that includes intermixed macroalgae as well as both *Spartina* grasses. In that respect, it is quite relevant to the current study. Salt marshes provide only 3.7% (Gouldsboro) and 2.6% (Dyer), respectively, of the productivity of these bays.

Planktonic Communities

We estimated the primary productivity of all planktonic communities in Gouldsboro Bay using chlorophyll concentrations and light penetration. Taking rocky intertidal productivity as the standard (described above), the ratios were used to

TABLE 2A. Algal biomass (g wet/m^2) of the hard-bottom communities at stations (sta.) throughout Gouldsboro Bay. Algal group designations are defined in Steneck and Dethier (1994) and shown in Appendix Table 2. See Tables 2B and 2C for dominant species: * for infralittoral zone see Table 2B; ** intertidal middle-depth algal group 5 is expanded in Table 2C. A dash (—) indicates no data; x = mean of stations for that location; sums are the combined means for the algal zone.

Bay location, sta. no., statistic	Intertidal zone biomass (by depth and algal group)													* Subtidal zone biomass (by depth and algal group)											
	High		Middle					Low						2.5 m				5 m				10 m			
	3	5	1,2	3	4	5**	6,7	1,2	3	4	5	6	7	1,2	3,4	5	7	1,2	3,4	5	7	1,2	3,4	5	7
Outer																									
7	—	—	145	145	280	13,420	0	167	1,926	3,098	3,182	58	2	31	73	10,323	16	285	2,136	11,819	40	72	54	142	120
8	—	—	112	136	551	11,651	0	41	118	2,265	5,067	7	1	37	86	12,144	16	224	448	10,528	118	33	8	210	118
x	—	—	128	140	416	12,536	0	104	1,022	2,682	4,124	2	1.5	34	80	11,233	16	255	1,292	11,174	79	52	31	176	119
Sum	—		13,220					7,966						11,363				12,800				378			
Mid to outer																									
11	—	—	4.3	0	91	22,605	0	51	0	1,020	11,606	0	25	420	2,280	3,300	86	—	—	—	—				
25	—	—	3.3	0	98	10,841	0.9	37	0	745	12,849	12	49	183	527	1,582	144	2	9	207	96				
23	—	—	56	0	203	24,524	23	14	0	434	15,609	0	11	—	—	—	—	—	—	—	—				
x	—	—	21.2	0	131	19,357	81	34	0	733	13,355	4	28	302	1,404	2,441	115	2	9	207	96				
Sum	—		19,590					14,154						4,262				314							
Mid to inner																									
13	—	—	129	—	47	38,760	0	0	0	198	13,990	0	17												
21	—	14,560	36	—	195	24,574	0	11	—	415	16,190	0	1												
x	—	—	82	—	121	31,667	0	6	0	306	15,094	0	9												
Sum	14,560		31,870					15,415																	
Inner																									
15	285	8,117	0	—	68	50,514	0	7	—	288	21,867	1	20												
19	2,300	8,627	24	—	84	68,313	0	7	—	31	20,159	0	0												
17	0	31,760	61	—	197	34,898	18	9	—	376	23,473	0	54												
x	1,292	16,168	28	—	116	51,242	6	8	—	232	21,833	0.3	25												
Sum	17,460		51,242					22,098																	

TABLE 2B. Infralittoral, dominant species composition in Gouldsboro Bay (g/m^2; after Adey and Hayek, 2005).

Species	Exposed	Mid bay	Protected
Chondrus crispus	4,300	4,000	2,300
Fucus distichus		~ minor component ~	

TABLE 2C. Middle intertidal algal group 5 mean dominant species composition in Gouldsboro Bay (g/m^2; after Adey and Hayek, 2005).

Species	Exposed	Mid bay	Protected
Ascophyllum nodosum	4,970	18,700	29,325
Fucus spp.	2,575	625	420
Chondrus crispus	215	105	20

estimate the productivity of the other communities (see Appendix Table 15). The resultant value of 0.06 kg/m^2/year was 17% of the 0.36 kg/m^2/year obtained using standard light/dark bottle ^{14}C methods. We use the ^{14}C numbers for our calculations of planktonic productivity in Table 3, as the results are comparable to the more chlorophyll-based work undertaken in Cobscook Bay by Phinney et al. (2004).

Planktonic productivity is significantly affected by turbidity, which strongly increases inland along the bay axes (Appendix). In the Gouldsboro–Dyer Bay complex, in-bay productivity is about one-half of that reported for the Cobscook study, whereas the outer (exposed) waters were nearly twice as productive as Cobscook waters. These numbers seem reasonable, considering the basic differences between the bays. Gouldsboro and Dyer Bays have a strong gradient of turbidity from the outer shores to the inner bays. Chlorophyll concentration was considerably higher in inner Goldsboro Bay, even though productivity, as measured with ^{14}C techniques, fell sharply, inversely proportional to increasing turbidity. The intertidal does not suffer from the turbidity problem, and because *Ascophyllum* survives well in silty environments, and remains abundant well into the upper reaches of Dyer Bay, intertidal productivity increases up-bay (Appendix Figure 64).

Using a mean specific phytoplankton productivity of 0.36 kg/m^2/year, at 7.8×10^6 kg/year for Gouldsboro Bay and 3.2×10^6 kg/year for Dyer Bay, phytoplankton provide approximately 24% and 16%, respectively, of the total productivity of the two bays. The greater proportion of Gouldsboro Bay primary productivity supplied by phytoplankton, as compared to Dyer Bay, derives from the greater open water area as compared to shoreline length.

TOPOGRAPHY

At mean high water spring tide (mhwsp) and 13.1 km axial length, Dyer Bay is 65% of the Gouldsboro Bay axial length at 8.5 km (Table 1). However, Dyer Bay covers only 42% of the total area relative to Gouldsboro Bay (11.9×10^6 m^2 and 28.3×10^6 m^2, respectively). In part, the difference is the result of postglacial "capture" of the adjacent Prospect Bay to the west by a recessional moraine blocking its potential mouth at Prospect Harbor; the shallow arm created includes Grand Marsh Bay and West Bay, together considerably larger than the equivalent northwest arm of Dyer Bay (Dyer Harbor). Dyer Bay has the contrasting Carrying Place Cove extending southeast opposite

TABLE 3. Primary productivity of marine communities of Gouldsboro (Goulds) and Dyer Bays. "Ratio re area" refers to productivity proportion of Dyer to Gouldsboro Bay relative to total bay area (e.g., in last row, Dyer Bay has 0.61 the productivity of Gouldsboro Bay but relative to its area, the productivity is 1.45 times higher); "tr" indicates trace amount.

Biological communities	Table 1 specific productivity (kg/m^2/year)	Total Productivity (kg/year × 10^6)				% Dyer/Goulds	Ratio re area
		Gouldsboro Bay	%	Dyer Bay	%		
Benthic							
Intertidal total	—	[16.14]	—	[8.76]	[44]	[0.54]	[1.29]
Rocky shore (*Ascophyllum*)	10.6	8.01	24.4	5.2	26.1	0.65	1.55
Rocky (miscellaneous)[a]	2	2.1	6.4	1.4	7	0.67	1.6
Mud and sand (with *Zostera*)	1.2	4.8	14.6	1.64	8.2	0.34	0.81
Salt marshes (*Spartina*)	1.73	1.2	3.7	0.51	2.6	0.43	1
Mussel beds (*Mytilus*)	0.2	0.03	tr	0.01	tr	0.33	0.8
Subtidal photic							
Kelp and *Zostera* beds	7.2[b]	[8.89]	—	[7.9]	[39.7]	[0.91]	[2.17]
3/4 kelp; 1/4 *Zostera*	5.7	4.5	13.7	6.4	32.2	1.42	3.38
1/4 kelp; 3/4 *Zostera*	2.7	2.4	7.3	1.3	6.5	0.54	1.29
1/8 kelp; 7/8 *Zostera*	2	1.5	4.6	0.13	0.7	0.09	0.2
Only *Zostera*	1.2	0.19	0.6	0	0	0	0
Armored and shell hash	0.1	0.3	0.9	0.07	0.6	0.23	0.6
Total benthic	—	25.03	76.2	16.7	83.9	0.66	1.6
Planktonic (whole bay: intertidal)	0.36	7.8	23.8	3.2	16	0.41	0.98
Total primary productivity	**—**	**32.8**	**100**	**19.9**	**99.9**	**0.61**	**1.45**

[a] "Rocky" intertidal minus rocky *Ascophyllum* (rockweed) patches (includes black zone, *Mytilus* zone, and sand and gravel patches; see text).

[b] Kelp only for this calculation.

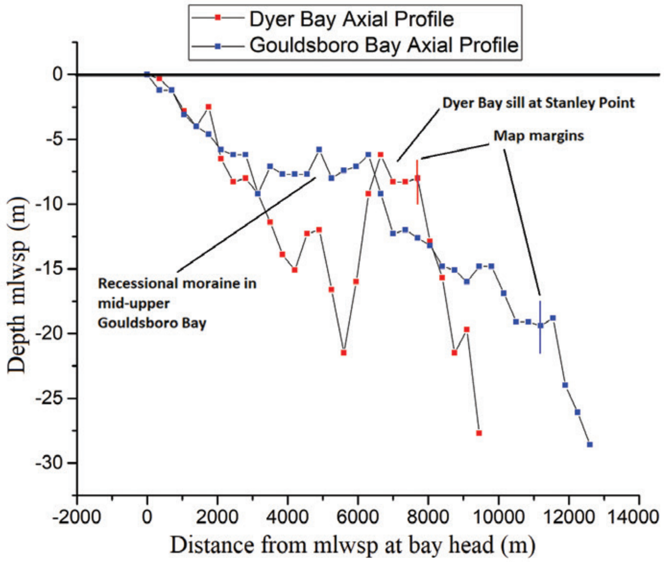

FIGURE 7. Axial profiles of Gouldsboro and Dyer Bays; mwlsp = mean low water spring tide. Recessional glacial moraines determine the bottom profiles of the two bays, but the locations of the moraines (mid- to upper bay in Gouldsboro Bay and bay mouth in Dyer Bay) produce very different profiles.

Dyer Harbor (and Gouldsboro Bay lacks an equivalent lateral arm), but it is considerable smaller than Gouldsboro's Grand Marsh and West Bays.

Axial profiles of the two bays are given in Figure 7. Although Dyer Bay is slightly narrower than Gouldsboro Bay (Figures 8, 9), and the depths are similar, the bottom topography is markedly different (Figure 7). The Dyer Neck recessional moraine causes a marked rise in the topography of the upper part of the main body of Gouldsboro Bay, providing a small basin southeast of Jordan Point. The equivalent "Yellow Birch Head" moraine in Dyer Bay lies at its mouth, creating a narrow constriction between Yellow Birch Head and Stanley Point. The net result is that there is a very shallow, barely noticeable basin in the upper part of the main body of Gouldsboro Bay, and the bottom profile slopes gradually from there to its mouth and beyond, whereas Dyer Bay has a distinctive basin in the lower main bay.

Hydrology and Wave Exposure

With a surface area, at mean spring high tides, of 12 × 10^6 m^2, and with a high tide volume of 80 × 10^6 m^3, Dyer Bay is smaller than the 28 × 10^6 m^2 area of Gouldsboro Bay, the latter having a high tide volume of more than 227 × 10^6 m^3 (Table 1). With roughly three-quarters of the centerline length and shoreline length, the area of Dyer Bay at high water spring

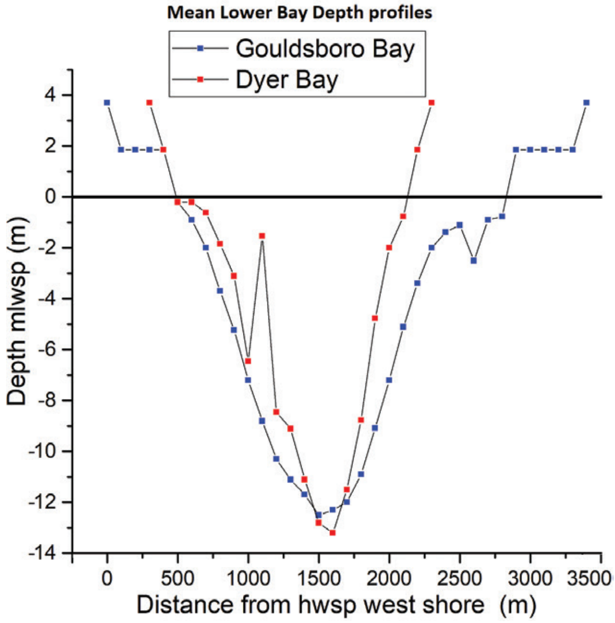

FIGURE 8. Mean lower bay depth profiles of Gouldsboro and Dyer Bays. Although the depths are the same, Dyer Bay is narrower and presents steeper profiles. Abbreviations: mlwsp = mean low water spring tide; hwsp = high water spring tide.

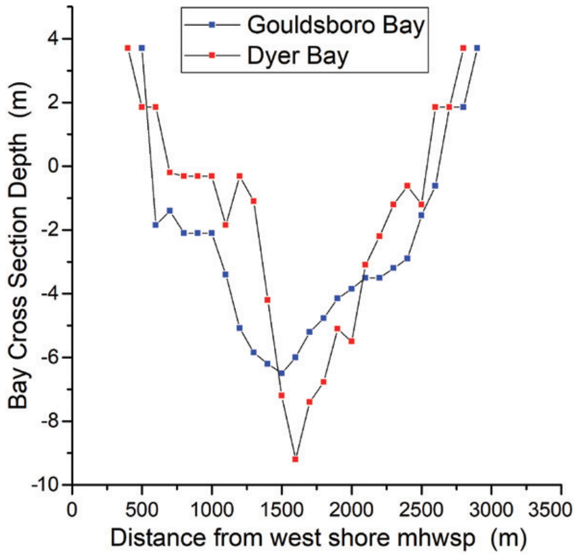

FIGURE 9. Mean mid- to upper bay profiles of Gouldsboro and Dyer Bays. Dyer Bay, with its sill produced by a recessional moraine at its mouth, retains its V-shaped profile. Gouldsboro Bay has a shallow basin in the upper bay because of the large Dyer Neck recessional moraine that crosses from northeast to southwest in the upper mid-bay. Map created by author WHA with Google Earth Pro.

tide is about one-third that of Gouldsboro Bay and at low tide about one-quarter that of the larger bay. Critically, despite having a substantially smaller volume, the shoreline of Dyer Bay is roughly three-quarters that of Gouldsboro Bay (Table 1); as we present below, it is the shoreline (both intertidal and shallow subtidal) which generates a substantial majority of the primary productivity in these coastal habitats.

Both Dyer Bay and Gouldsboro Bay experience a high degree of tidal flushing. At spring tides, about 29% of the water in Gouldsboro Bay is exchanged, and nearly half (48%) of Dyer Bay is exchanged on each spring tide. Bay volumes and tidal flushing with moderately high nutrient coastal water, as already described, provide the key to the essential lack of nutrient control over primary productivity and to the structuring of the ecosystems of the bays. As described for Cobscook Bay (Larsen, 2004) and noted above, it is the offshore GOM dynamic oceanography that provides this nutrient-rich environment. The strong tidal currents peculiar to the eastern Gulf (resulting from the volume and shape of the Gulf/Bay of Fundy complex) have ensured in the past that the seaweeds in this bay complex have not been nutrient limited. Considering the long shorelines for both bays, and the rich intertidal and subtidal macroalgal and eelgrass standing crops, along with considerable water movement caused by the large tides, nutrient supply provides little constraint to primary productivity.

The intense wave action of the outer coast, especially in winter, removes a considerable amount of algal biomass from the rocky substrate (see Appendix). Intertidal standing stock biomass along the outer coast was roughly half that observed in the lower bays, and total algal productivity, largely from *Ascophyllum*, is 20%–50% lower than in the bays. In the exposed subtidal, kelp standing crops at 2.5 and 5 m depth and productivities are two to three times higher in summer than in spring, when biomass is reduced (see Appendix Figures 76–78). Rates of primary productivity are significantly higher on outer bay shores than further into the bays, partly caused by the lack of intense in-bay wave action to provide mixing, and increasingly up-bay by the lack of hard substrate. On the other hand, individual *Ascophyllum* and kelp plants can demonstrate multiyear longevity in the bays when not subjected to human activity (Gendron et al., 2017).

Community Structure and Distribution

A combined Gouldsboro/Dyer Bay ecological community map, based on Google Earth Pro analysis, is given in Figure 4. Close-ups of selected areas, at lower sight altitudes, are shown in Figures 5 and 6. The collated whole bay areas of the ecological communities are given in Table 1. The typical distribution of seaweed and *Zostera* communities relative to geomorphological substrate is shown in the Appendix (Figure 53).

The remapping of Gouldsboro Bay with Google Earth Pro differs somewhat from the 1980s survey as the result of finer-grained analyses and, subsequently, increased spatial precision. The total area of the bay was increased by 34%, but the subphotic, silt/mud open water bottoms constitute three-quarters of that increase. In the productivity analysis, this provided more phytoplankton production; however, the low specific productivity of phytoplankton resulted in little change in the analysis presented here as compared to the 1982 report. With the greatly improved areal visibility, habitat previously characterized as "rocky intertidal" was further subdivided into *Ascophyllum*-covered rocky patches, mats of the red seaweed *Chondrus crispus*, and the high and low tide bands of the black and barnacle zones, mussel bands, and interspersed sand patches referred to as "rocky (miscellaneous)." Although this characterization reduced the rocky *Ascophyllum* zone (as compared to 1982) by 40%, and the miscellaneous intertidal was allocated a productivity of only 20% that of the *Ascophyllum* zone, total intertidal productivity was little affected because mudflats (with *Zostera*) and salt marsh areas increased when measured in the satellite images. A visual comparison with the 1980s approach can be seen in Appendix Figures 18, 19, and 53.

DISCUSSION

The extensive benthic analyses presented in the Appendix for Gouldsboro Bay parallel the more recent research published for Cobscook Bay in most aspects (Larsen, 2004). Although the planktonic research presented in this study is considerably less extensive than that of the Cobscook Bay project, it is very much in agreement with that study, in its basics, and thus is applicable to the whole bay analysis that we provide in this paper.

As in Cobscook Bay, benthic macroalgae, and to a lesser extent *Zostera*, contribute more primary productivity to the system than do the phytoplankton; also, as in Cobscook Bay, nutrients are generally not limiting because of the constant tidal-driven supply from large-scale "upwelling" in the GOM (Garrett et al., 1978; Townsend et al., 1987). Benthic primary productivity, mostly by *Ascophyllum*, the kelps, and *Zostera*, provide 76% and 84%, respectively, of Gouldsboro Bay and Dyer Bay productivity. Clearly these are benthic-driven systems, with Dyer Bay being more strongly benthic because of its higher coastline-to-area ratio.

Although the tidal range in the Gouldsboro–Dyer complex is about 60% of that in Cobscook Bay, the Gouldsboro–Dyer complex, unlike that of Cobscook Bay, is partially open to the Atlantic Ocean. On the Maine coast, wave action produces the rocky bottoms necessary for a considerable development of macroalgae. Tidal current action is not nearly as effective in producing rocky bottoms; where tidal action is effective in these bays, in forming pebble/shell armored bottoms, only the low-producing coralline algae can successfully colonize. Local in-bay wave action can be important in driving primary productivity in the rocky intertidal and even shallow subtidal zones. However, although Cobscook Bay is several times larger than Gouldsboro Bay, it is broken up into narrow sub-bays, so local wave action is minimized.

Wave action is a driving force in subtidal macroalgal primary production (Leigh et al., 1987; Doty, 1971; Suskiewicz et al., in press). In Gouldsboro Bay, there is a substantial difference in productivity rates and seasonal biomass loss between the outer coast and inside the bay (see Appendix Figures 60, 76–79). Higher productivity by kelps occurs in the subtidal at the more exposed locations, despite greater standing crop loss. The situation is reversed in the intertidal because *Ascophyllum*—the primary intertidal producer—is less resistant to wave action; thus removal of plants by wave action (especially in winter) in the more exposed areas greatly reduces productivity. The inner, partially protected areas of these bays have the greatest intertidal standing crops and highest net productivities. The uppermost reaches of the bays, with no open water wave action, are largely depositional environments characterized by mudflats, salt marshes, and soft bottom subtidal. Rocky, mostly cobble "bars" are scattered in the upper reaches of the bays, and *Ascophyllum* (rockweed) develops on those "bars" (Figure 6); however, this represents only a very small part of the bay surface. *Zostera* and microalgae provide only a minimum level of primary productivity in these protected environments. Salt marshes, while moderately productive, do not attain the higher levels of kelps and *Ascophyllum*, with only 2%–4% of bay productivity, respectively. As most of that productivity is retained within the marshes, even this low level is likely a trace component of the total energy budget of the broader bay.

We do not update the preliminary systems analysis, based in biomass transfers, that was presented in the Appendix (see Appendix Figure 90). Biomass transfers are likely more suitable to understanding human perturbations and climate change, and that analysis, as it stands, will support the future development of an energy-based model. As the Appendix model presents, macroalgal biomass, when torn from the substrate by wave action, grazers, or other perturbation, ultimately breaks down to particulate detritus on the bay bottoms, particularly on the upper sections of cobble and gravelly beaches. These bays are detrital systems largely based in the very large primary production by seaweeds (and to a lesser extent by *Zostera*), both intertidal and subtidal. Most of this production remains in the bay on the silty deeper bottoms and on the mudflats, where it provides particulate food for a great diversity and biomass of invertebrates, as described in the Appendix. The percent of organic compounds in the bottom sediment increases landward, from about 2% in the lower bays to more than 10% on the mudflats; clearly, there is a hydrographic mechanism driving organic detritus landward to the flats (see Appendix).

Comparison of Productivity of Gouldsboro and Dyer Bays

As we have shown, Dyer Bay has only 42% of the area of Gouldsboro Bay (Table 1), yet, using the same specific primary productivities for each community in both bays, Dyer Bay has 45% greater productivity per unit area (as shown at bottom of the far right column in Table 3). This greater productivity is almost entirely the result of the larger fraction of rocky intertidal and subtidal habitat in Dyer Bay compared to Gouldsboro Bay (Table 1). This difference derives mostly from two factors: an 80% greater shoreline length for Dyer Bay (in proportion to bay area) and a smaller proportion of highly protected, lower productivity up-bay areas compared to Gouldsboro Bay.

Our productivity analyses indicated that total benthic primary productivity is more than an order of magnitude higher than total phytoplankton productivity in bays along this region of the Maine coast. In general, the narrower a bay, the greater will be the proportion of benthic shore, both intertidal and subtidal, and the greater will be the total bay productivity. Bays with abundant islands also tend to be highly productive because of the greater shore lengths. However, it seems likely that there is a limit to this rule in that lack of in-bay wave action, increased silting, and reduced wave energy contact will reduce both macroalgal standing crop and productivity.

Plankton primary productivity in the Gouldsboro–Dyer complex was measured at 36.5 g C/m^2/year, far below the estimate of 150 g C/m^2/year provided by the Fish and Wildlife Service for coastal Maine. This difference can be explained by light attenuation within the bay caused by high turbidity. Large bays such as nearby Frenchman's Bay will have a far lower primary productivity as they are highly phytoplankton dominated by their greater average depth and lower ratio of shallow coastline to surface area. Even though more open to wave action than bays such as Gouldsboro and Dyer, the considerably higher primary productivity of wave-exposed subtidal kelp in Frenchman's Bay may be offset by the lower productivity of intertidal *Ascophyllum* caused by wave damage. All these factors must be taken into account when accessing the susceptibility of Maine bays to anthropogenic perturbation. Western Maine bays, which have a much smaller tidal amplitude coupled with higher summer water temperatures, which can be stressful to kelp productivity, may fundamentally differ in their primary productivity.

Resampling Efforts in Gouldsboro Bay and Comparisons across Decades

As described in Materials and Methods, most of our data and analyses regarding the biological communities of Gouldsboro bay were collected in the 1980s whereas the data from Dyer Bay were from 2009. Because the areas of dominant communities have been remeasured as part of this study, only changes in standing crop and productivity would affect our analyses with time.

As indicated in our Introduction, the GOM has undergone extraordinary changes in the past several decades. To address the temporal differences in our sampling, we resampled the rocky benthic stations and several of the soft bottom stations in Gouldsboro Bay in 2017 as well as the entrance to Dyer Bay. Although changes in biota, which are described in detail in upcoming manuscripts, are not the focus of this paper, we can offer the following observations. As is the trend throughout the GOM, sea urchins have become rare or absent throughout the Gouldsboro–Dyer Bay complex; urchins were rarely encountered during any of our 2017 sampling. Both lobsters and crabs (*Cancer borealis*, *Carcinus maenas*) were common, and fishing pressure has increased substantially, as evidenced by landings data (DMR, 2018) and the number of lobster traps set throughout both bays (WHA, personal observation). The intertidal zone continues to be dominated by *Ascophyllum nodosum*, as our surveys in 2009 and 2010 demonstrate. Subtidally, the seaweed assemblages continue to be a mixture of Subarctic and Boreal species, although with a measurable reduction of several Subarctic species. Our most recent surveys did not detect any of the more recently introduced invasive algae (e.g., *Dasysiphonia japonica*), which are having an impact on communities of the southern Gulf (Dijkstra et al., 2017). Curiously, much of the rocky bottom habitat in deeper water was coated with a thin layer of fine sediment and barnacles. As we will show in a future publication (Adey and Suskiewicz, unpublished data), many coralline-covered rock samples collected from exposed sites in the 1960s were almost entirely devoid of subtidal barnacles; similar samples taken in 2017, from the same stations, were often densely coated with these filter feeders. This suggests an increase of both sedimentation and nutrient concentrations in the water column.

Although there do not appear to be major changes in macroalgal and *Zostera* biomass and productivity since the baseline data were collected in the 1980s, the bay-wide productivities presented here represent the status of these bays in the 1980s. In that respect, they are a valuable baseline against which to compare future ecosystem function.

CONCLUSIONS

Our analysis of Gouldsboro and Dyer Bays highlights the contributions of benthic primary productivity to ecosystem function on the eastern Maine coast, and especially demonstrates the role of underlying geology and glacially derived topography in shaping ecosystem structure and function. The large (4.2 m) tidal fluctuations aid water column mixing and prevent nutrient depletion in these otherwise narrow bays; however, coastal water column mixing likely will not offset human-derived eutrophication because of the primary coastal water source in deep shelf waters and the secondary source from the Gulf of St. Lawrence. The results presented here, and in the Appendix, will provide an effective baseline for detecting ecosystem changes going forward; however, because of the ever-increasing utilization of marine resources by coastal populations, it is essential that similar baseline studies of system function be established at several localities along the entire length of the Maine coast.

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Appendix: A Resource Assessment of Gouldsboro Bay, Maine

The following pages contain the first author's original 1982 ecological analysis report on the Gulf of Maine to the National Oceanic and Atmospheric Administration. The report was not originally intended for viewing two-page spreads of a hand-held booklet, so left–right pagination was not consistent. Only pages with report text were numbered; pages with figures and tables were not paginated. The report's original pagination is retained herein as displayed at the bottom center of each page that was numbered.

A RESOURCE ASSESSMENT OF
GOULDSBORO BAY, MAINE:

An Ecological Analysis of a type bay in the Gulf of Maine

A Report to the
National Oceanographic and
Atmospheric Administration
Marine Sanctuary Program

Walter H. Adey
Marine Systems Laboratory
Smithsonian Institution
Washington, D.C.
1982

Infrared satellite photograph of Gouldsboro area.
The tide is relatively high, and only a small part of the rocky intertidal is exposed. However, the bright red color of those areas is indicative of the high chlorophyll levels and the resulting high primary productivity.

CONTENTS

INTRODUCTION

The purpose of this study is to develop an ecological assessment of Gouldsboro Bay in Washington County on the eastern coast of Maine. The assessment is in part descriptive of geological, hydrological, chemical and biological elements, but its primary focus lies in a systems-type analysis of bay function.

This investigation as a whole has drawn heavily from on the 1980 Fish and Wildlife Service treatise, "An Ecological Characterization of Coastal Maine." That six volume review provided the working base for this study. No attempt is made to determine or list all of the taxa of the bay and reference is made to volume four of the above indicated set for a species list for the Maine Coast. Ecologically, this paper deals primarily with the major elements of trophic and community structure.

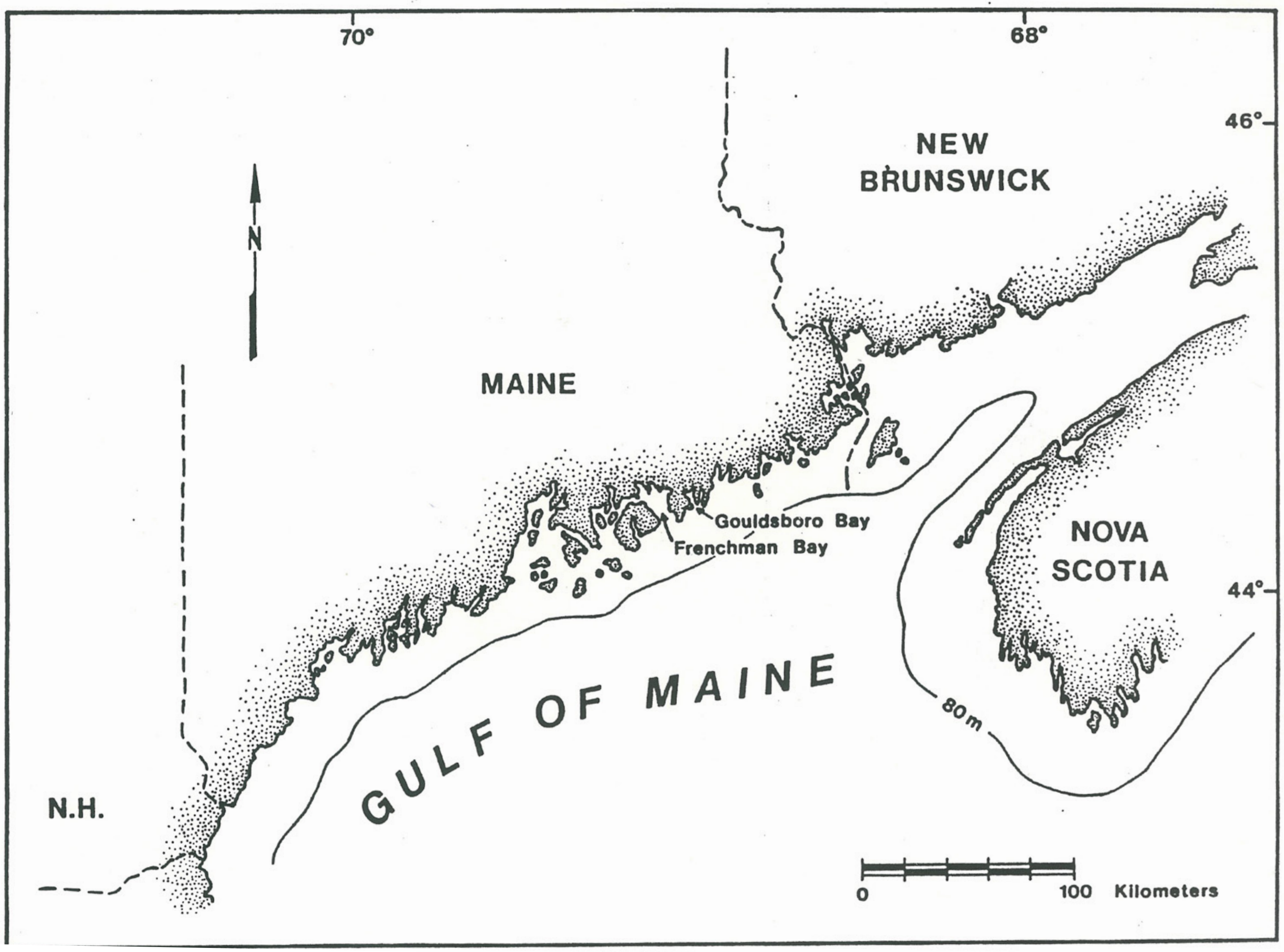
The field work for this paper was primarily carried out during the late summer and autumn of 1981 and 1982. A two-week winter field session was completed in February-March 1982. The long 1982 summer session in 1982 concentrated on benthic community structure.

GEOGRAPHY

Gouldsboro Bay is located on the boundary line between Hancock and Washington Counties, Maine on the north central coast of the Gulf of Maine at latitude 44° 27' N and longitude 67° 58" W (Figure 1). This is a submerged glaciated coast, and consists of a maze of islands and bays (Figures 2 & 3). The outermost islands are rocky and tend to be rather barren and wave beaten(Figure 4); the inner portions of the bays and have mud flats (Figure 5) and occasional salt marshes (Figure 6). Most of the coastal area (90%) is in spruce-fir and mixed hardwood forest, which generally extends to the shore (Figure 7). The population level is generally low, 40-100 persons per square mile (depending largely on the season). A large part of the local population is self-employed, subsisting on a mixture of fishing and small scale forestry.

Gouldsboro Bay itself (Figures 8-11) is oriented roughly on a north-south axis; it is approximately 6.5 nautical miles (9.5 statute miles; 13 km) long, and its main section is one nautical mile (1.2 statute miles; 2.1 km) wide. The maximum depth of Gouldsboro Bay is 70 feet (23 m). Although a few shallow basinal areas are present, the bottom generally slopes gradually from the upper end to the mouth of the bay. Fresh water streams entering the bay are generally quite small in size and except near the mouths of the streams , the salinity ranges from 30 - 32%. The tide range is roughly 8-12 feet (2.5-4m). The shores are

Figure 1. The northern Gulf of Maine showing the Gouldsboro Bay area.



generally rocky, although mud flats and sandy silts dominate the upper reaches and the floor of the bay. A few small marshes are present in the upper reaches. The shores of the bay are generally forested. Corea (Figure 12), a small fishing village of about 400 people, lies just off the southwestern corner of the bay, and Steuben (Figure 10), a town with a population of about 970 people, lies on Tunk Stream at the northeastern corner of the bay. Small homes are scattered along the shores of much of the bay. Lobster fishing and clamming is extensively practiced in Gouldsboro Bay, largely by individual fisherman. Three semi-permanent fish weirs for herring are present in the bay. However, Gouldsboro Bay is not locally regarded as a good bay for herring, and catches tend to be small. During the winter, scallop dragging is sporadic but sometimes intensive.

Figure 2. Aerial photograph of the Pleasant Bay/Western Bay area just to the east of Gouldsboro Bay.

Figure 3. Inner end of the Bay complex in the same area showing typical mud flat/tidal stream situation.

Figure 4. Exposed rocky shore - Moose Peak light on Mistake Island.

Figure 5. Mud/flat fringing marsh complex in Washington County. Taken in spring.

Figure 6. Mill River - one of the few, well-developed marsh complexes in eastern Maine.

Figure 7. In protected areas of bays, the forest extends nearly to high tide line.
In many locations, stumps can be found in the intertidal.

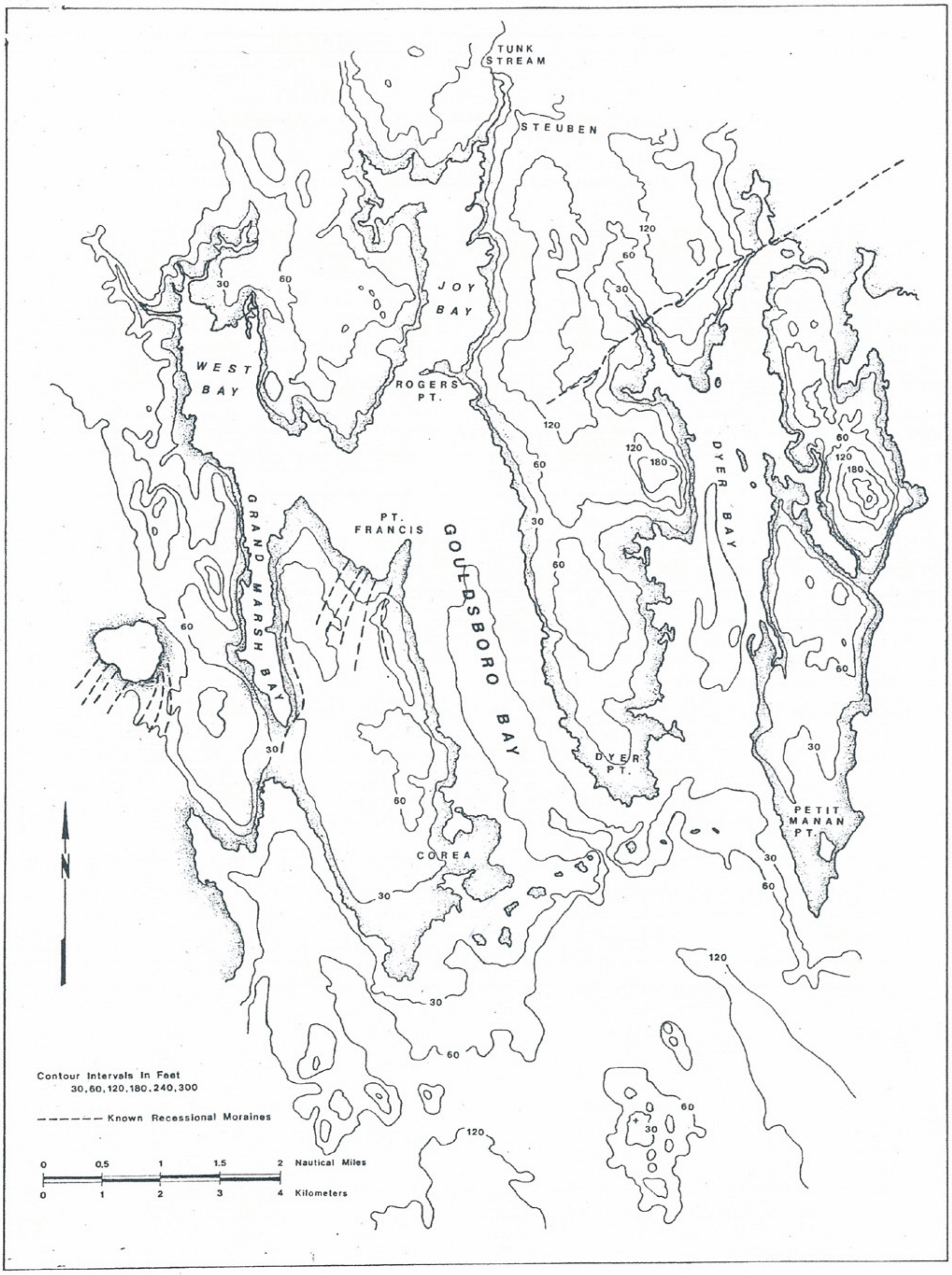


Figure 8. Topographic map of the Gouldsboro Bay area.

Figure 9. Gouldsboro Bay from offshore showing the inshore and bay regions

Figure 10. The inner end of Joy Bay and Gouldsboro Bay
showing Tunk Stream and the town of Steuben.

Figure 11. Close in aerial of Gouldsboro Bay looking north; the islands at the mouth of the bay appear in the foreground.

Figure 12. Village of Corea near the mouth of Gouldsboro Bay (upper right).

MATERIALS AND METHODS

The field work for this investigation was undertaken during the summers of 1981 and 1982 and the fall and winter of 1981 from small boats based from the Smithsonian Institution's Marine Systems Laboratory (MSL) research vessel the Marsys Resolute (Figures 13-15). Underwater work was primarily accomplished through the use of SCUBA (Figures (15-17). Mapping was based on NOS nautical chart 13324 and a low tide photomosaic made from 9x9 black and white aerial photographs taken on May 16, 1944, by the former Coast and Geodetic Survey. Station locations for the 1981 summer session are shown in figures 18 and 19. Several aerial observation and aerial photographic missions were flown using the MSL Albatross Amphibian (Figure 13).

Geological studies were based on aerial survey, surface reconnaissance, gouge augers (Figures 20, 21), vibracores (Figures 22, 23) and seismic profiling. Surficial sediment samples were collected with a Van Deen - type grab. A Blutworth ES-130 precision depth recorder and an Alden OSR 19T seismic profiler were used to delineate surface and subsurface depth and stratigraphic information. Suspended sediments were collected with a Niskin water sampler and filtered through a 47mm diameter 0.45u pore size millipore membrane filter.

Temperature/salinity data were taken using a Beckman PS5-3 induction salinometer (Figure 24). The tide gauges are Leopold and Steven model A-71 (Figure 25). Current information was

Figure 13. 100 ft Research ship Marsys Resolute used to carry out research in Gouldsboro Bay.

Figure 14. Boston Whaler used for a variety of work from diving to coring.

Figure 15. Inflatables were used for a large part of the benthic studies.

Figure 16. Benthic studies crew unloading gear at the end of a dive.

Figure 17. Bay temperatures in winter are generally less than 0oC and require special gear for efficient working.

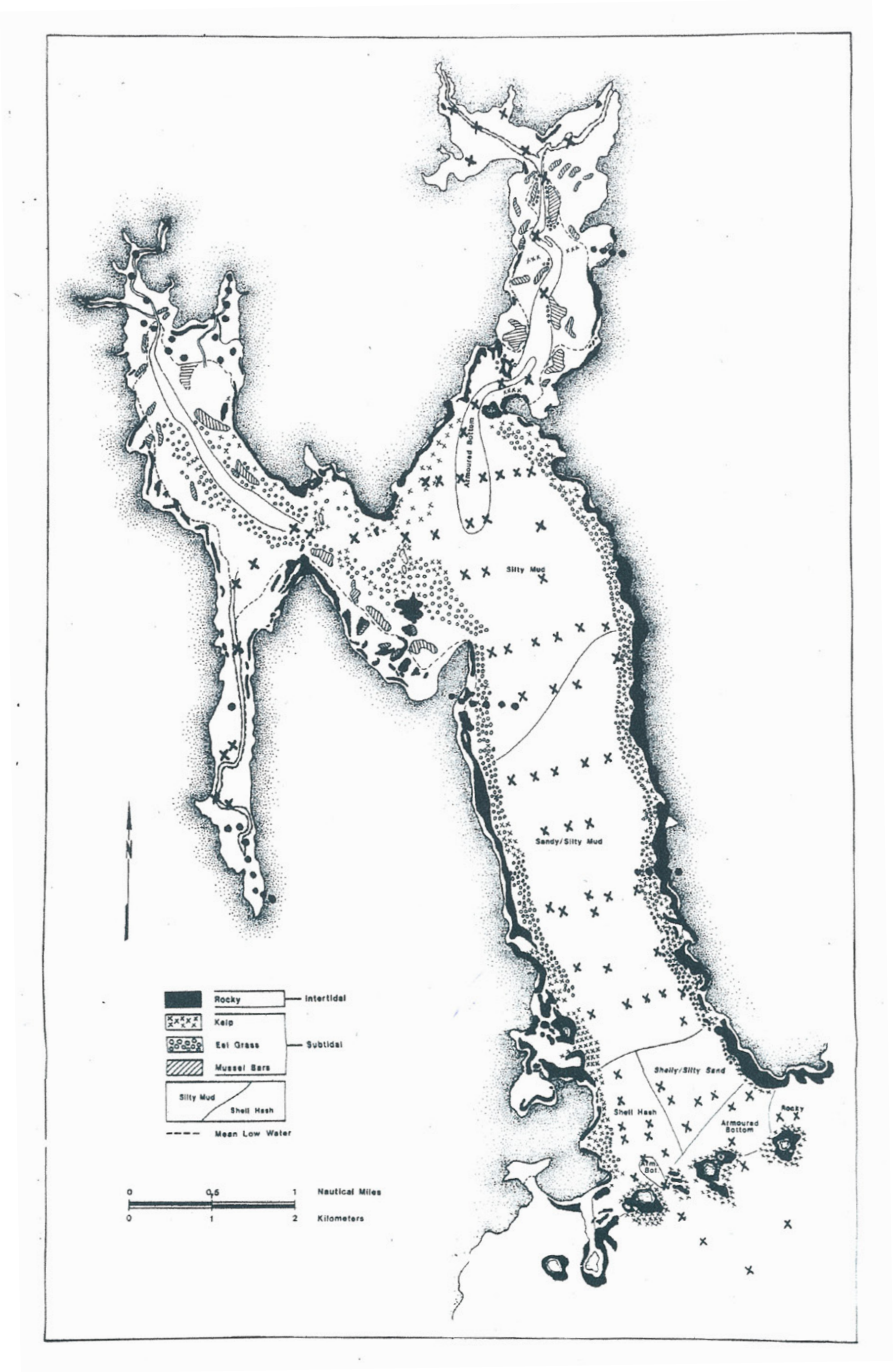


Figure 18. Base map of Gouldsboro Bay showing geological stations. Sediment samples x; Cores.

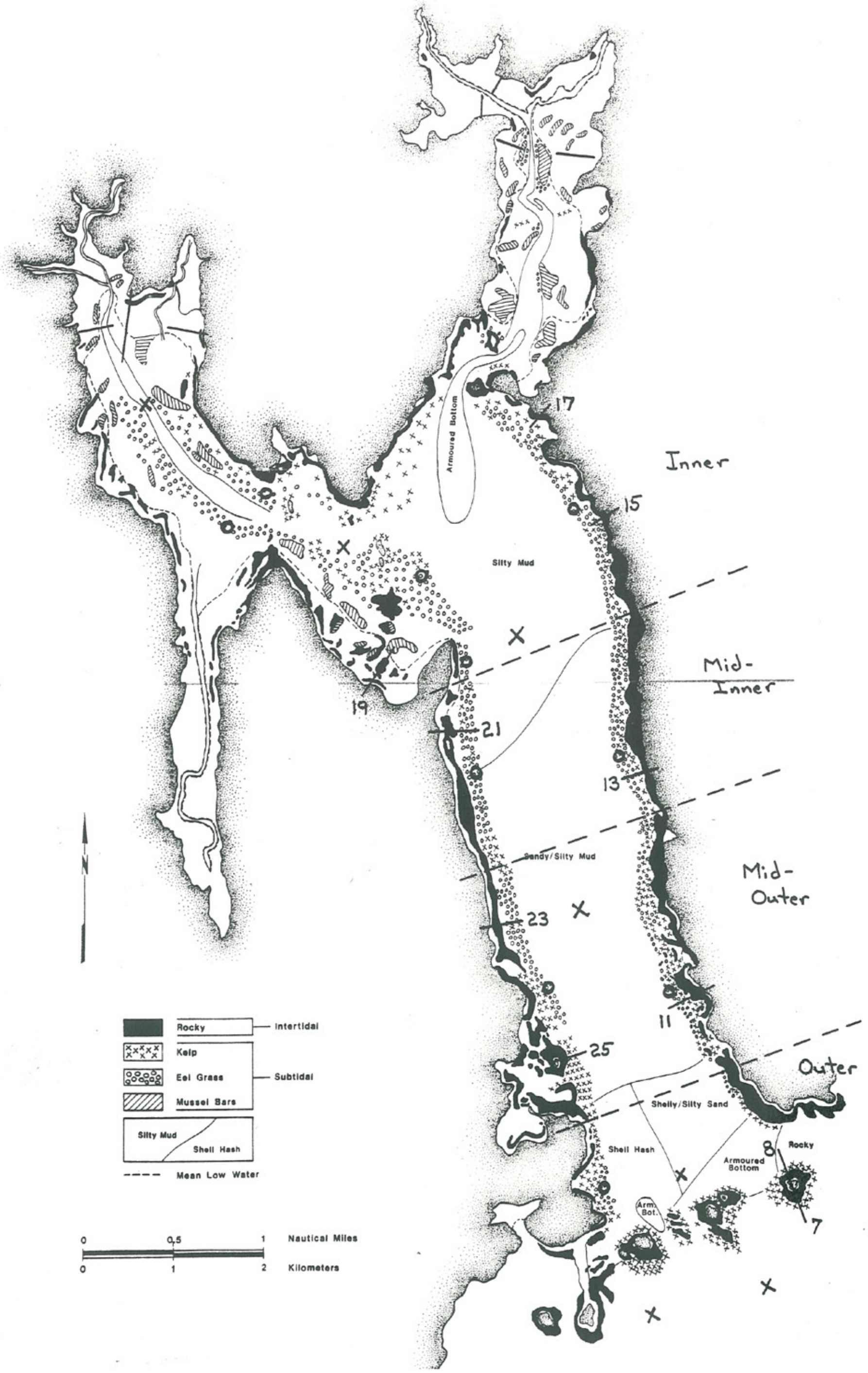


Figure 19. Base map of Gouldsboro Bay showing biological stations. Benthic transects _____5; Zostera stations O; Plankton stations X.

Figure 20. Auger coring for locations of Presumpscot clay near the forest/Great Marsh boundary.

Figure 21. Removing and packing section of Presumpscot clay from a beach core.

Figure 22. Setting up tripod to remove core barrel.

Figure 23. Core barrel with 5m long core of marsh peat following extraction.

Figure 24. Taking temperature/salinity profiles with the Beckman salinometer.

Figure 25. Tide station on lobster boat pier at the northwestern corner of the main bay.

obtained using arrays of General Oceanic 2010 film recording current meters. Nutrient data was collected by freezing water samples and returning them to the MSL laboratories in Washington, D.C. for calorimetric analysis.

Soft bottom benthic samples were taken with a box core (Figure 26- 27). A 1/16m^2 tossed quadrant was used for all hard bottom benthic population and biomass sampling (Figures 28, 29). At each station/bathymetric level, 5-10 quadrants were thrown. Community and population content of photosynthetic pigment was determined in the field using calorimetric analysis on a Beckman DU spectrophotometer.

Plankton collections were made by towing nets of 80um and 150um mesh from a small boat. Phytoplankton primary productivity was determined by the C^{14} method using a Packard 2660 liquid Scintillation Counter.

Bay export data in the form of fishery landings were obtained by extensive interviews with fishermen, dealers and wardens during both the summer and winter field sessions. Control of the data was based on Maine county fishery landing statistics provided by the State of Maine Department of Maine Resources.

Figure 26. Box-coring on a Joy Bay mud flat.

Figure 27. Sampling box core for chlorophyll concentration.

Figure 28. Typical dense Ascophyllum nodosum (rockweed) bed in the mid-intertidal of mid Gouldsboro Bay

Figure 29. Establishing grazer feeding cages in the Gouldsboro Bay intertidal.

CLIMATE, WEATHER AND BIOGEOGRAPHY

The Maine coast, being a continental shoreline lying at moderately high latitudes in the westerlies, and being positioned on the western side of an ocean, is strongly continental rather than oceanic in character. Even though the immediate coast has a near-maritime climate, the temperature is characterized by extremes and the weather by a succession of bi- or tri- weekly lows and fronts moving off the continent. The weather tends to be changeable on a one to four day cycle. Except along the immediate coast, summers tend to be warm with air temperatures generally between 60-80° (20-30°C). Yearly rainfall is moderate, between 40 and 50 inches, and the drainage tends to be poor due to the till surface and often underlying clay. Bogs, lakes and small streams are abundant and the vegetation is rather lush (Figure 30). On the immediate coast the autumn is early (Figure 31), although it is pleasant and long-lived. An occasional intense storm of wind and rain can be expected in November and December and it can have a strongly modifying effect on the shoreline (Figures 32, 33). Significant snow and low temperatures usually do not develop until near the end of December; however, January and February can be quite cold with temperatures often well below 0°F (-15°C) (Figures 34, 35). Also, in the spring, March is generally a winter month; low water temperatures and considerable fog persist through June and into July, and even August (Figure 36).

Figure 30. Grand Marsh in early summer, looking south. Note the now-unused dike in the foreground.

Figure 31. Grand Marsh, looking north, taken in early October. The foliage change is well underway.

Figure 32. Islands at the mouth of Gouldsboro Bay during a period of heavy seas in September.

Figure 33. Cobble/boulder berm in exposed cove at the southern end of Dyer Neck. These berms are maintained and slowly driven landward by a combination of slowly rising sea level and a few intense winter storms.

Figure 34. Late winter on the upper end of West Bay. West Bay and Joy Bay are frozen over during an average winter.

Figure 35. Western shore of the main section of Gouldsboro Bay during an early March northwester. The main bay will sometimes freeze on a calm night in late winter, but generally it is the province of loose pack ice.

Figure 36. Fog bank ‘hanging’ offshore in July. In the Gouldsboro area, a slight shift to the south under hot humid conditions inland will bring dense fog over the entire bay.

Figure 37. Ice limit in Joy Bay, the first week in March, 1982.

The waters of the Coastal Gulf of Maine, like the Gulf of St. Lawrence, are generally characterized by a wide temperature range, with bay surface waters typically reaching temperatures over 15°C in the summer and below 0°C in the winter. The more protected harbors, bays mud flats and marshes typically develop and maintain several feet (0.3 -1m) of ice from January to March (Figure 37). Mid-bay areas are often characterized by drifting ice pack (Figure 38) although water temperatures outside the bay are usually 0°C or above and pack ice and shore fast ice in any quantity are absent (Figure 39).

The basic water climate and flora and fauna of the Maine coast are subarctic in character, and along with the remainder of the coast from Cape Cod to Newfoundland is closely related to the Okhotsk Sea and western Bering Sea in the north Pacific. On the other hand, the strong tidal character of the eastern Gulf of Maine has a significant influence on the water climate and on the flora and fauna. Tidal mixing tends to reduce the development of stratification in summer and prevent the development of very cold surface water temperatures outside of bays in the winter. Offshore and more eastern areas in the Gulf tend to have narrower temperature ranges, from 0° to 3.0^0C in winter and 10-12°C in summer. Thus, there is a boreal element to the flora and fauna which is matched in southern Iceland, the northern British Isles and in the outer Norwegian Coast. In addition, the high water temperatures in the southwestern Gulf of Maine and in some inner

Figure 38. Mid-bay ice pack and shore-fast ice lip (in distance), the first week in March, 1982.

Figure 39. Outer, open shore, the first week in March, 1982. No shore front ice (ice lip) is present on the exposed coast, and only an occasional piece of pack ice from the adjacent Bay is brought out by wind and tide.

Maine bays in summer allows for the occurrence of temperate elements from south of Cape Cod as relicts, occasionals or introductions.

Thus, the biogeography of the coastal Gulf of Maine is complex and includes subarctic, boreal and temperate biotic elements. Nevertheless, the boreal and temperate elements have been over-stressed in the past, probably because of the scientific preoccupation with the plankton and the quite mobile organisms of the fishery. The basic biogeographic character of the coast is subarctic. (Figures 40, 41).

Gouldsboro Bay, lying well to the northeast in the Gulf of Maine and being in an area of east-west trending shoreline, is influenced by strong tides, winds off the water in the summer and winds off the land in the winter. Thus, it is relatively cool and has a narrower temperature range than the southwestern portion of the Gulf of Maine. Based on area coverage of the long-lived, sublittoral sedentary coralline flora, the outer coast in this area is about 65% subarctic, 30% boreal and 5% temperate in character. The inner reaches of bays, where a hard bottom exists, are 75% subarctic, 5% boreal and 20% temperate in nature.

GEOMORPHOLOGY AND SEDIMENTOLOGY

In the area of Gouldsboro Bay, the bedrock geology consists primarily of mid-paleozoic granites and granodiorites that have

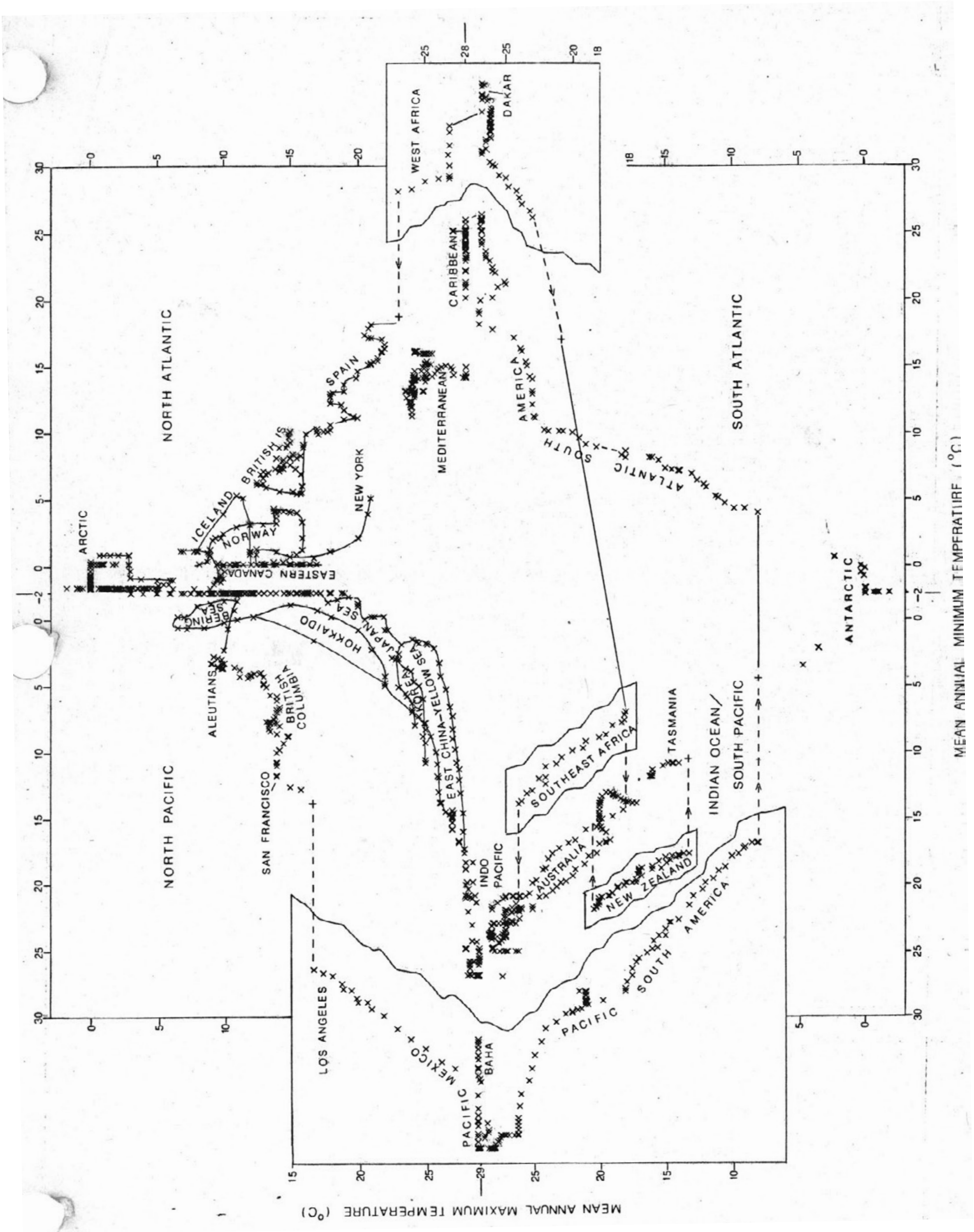


Figure 40. Mean maximum, me minimum coastal temperature framework for the world ocean. Note that at 12-50C mean max. and 00C (mean min.), Gouldsboro Bay would place in the middle of the eastern Canada shores temperature regime. Winter temperatures in Europe are generally warmer (boreal). After Adey and Steneck).

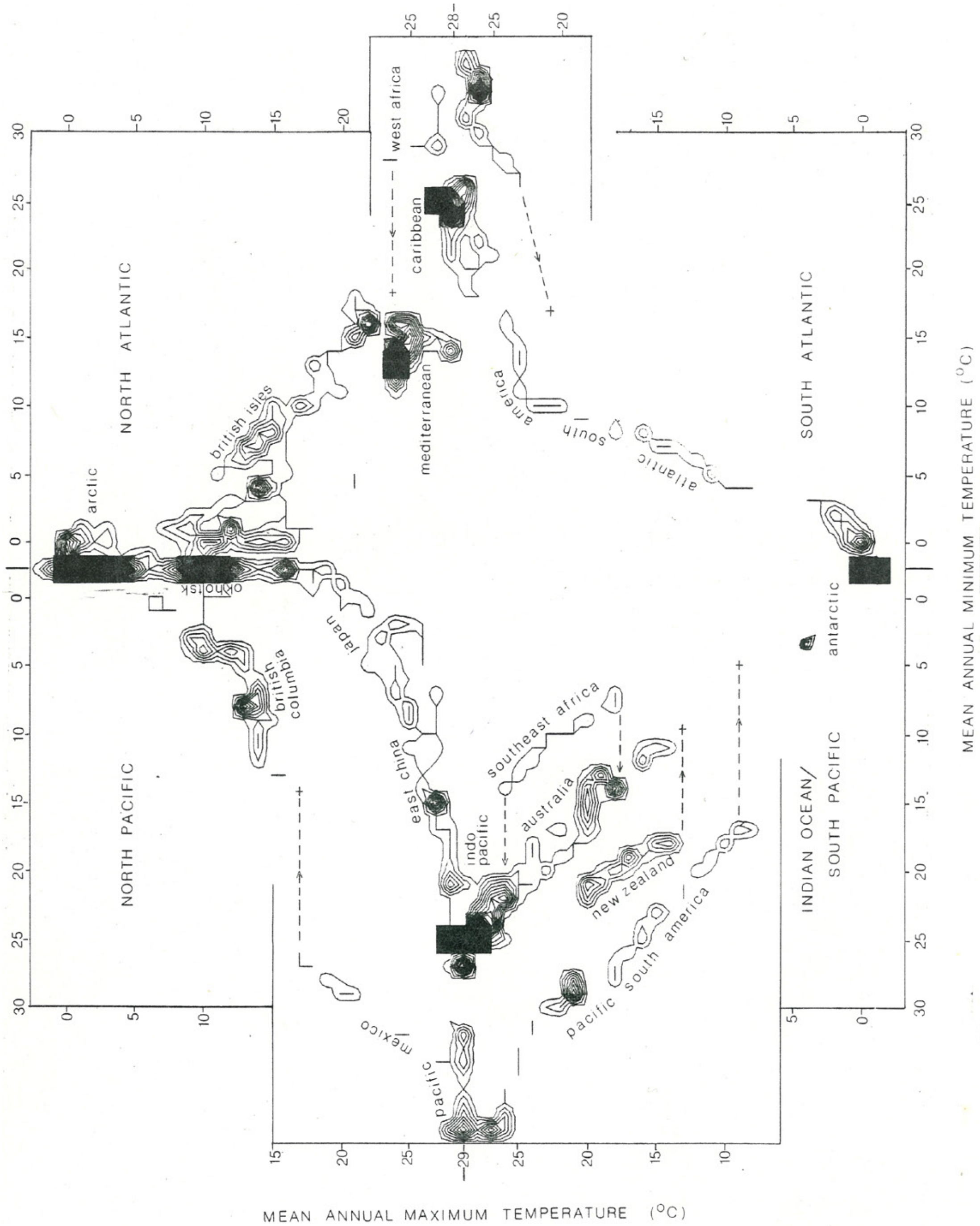


Figure 41A. Contours of area of mean maximum and mean minimum temperatures for unit 60 nautical miles of coast. Note that Gouldsboro Bay is placed In a small North Atlantic equivalent of a large North Pacific subarctic which includes the Okhotsk Sea.

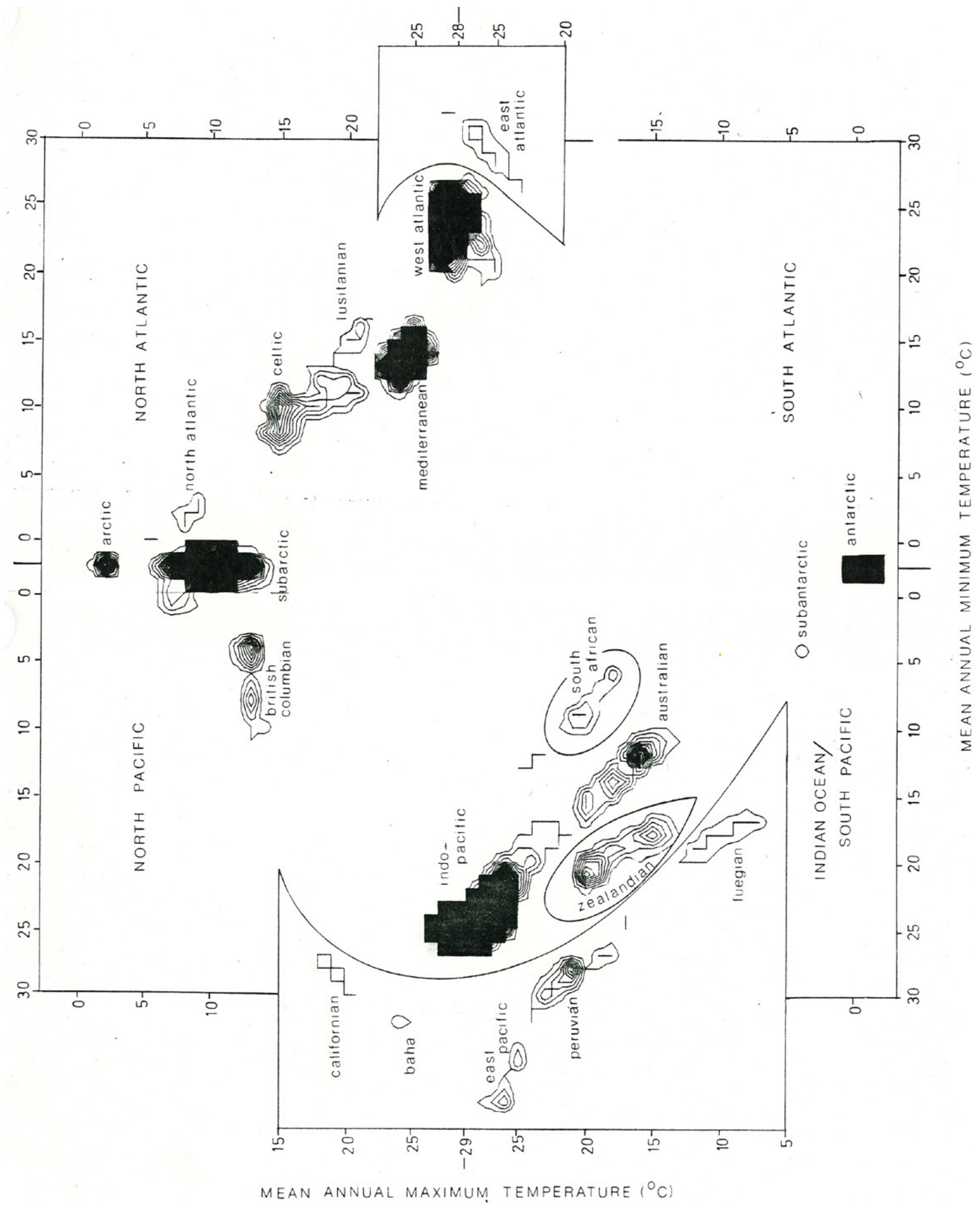


Figure 41B. Mean coastal temperature framework for the Pleistocene. The North Atlantic Subarctic is not a major element. Thus, the eastern Gulf of Maine, along with the Gulf of St. Lawrence, Nova Scotia and Newfoundland is dominated by a (North Pacific) Subarctic biota with a small component of Celtic (boreal) elements.

been smoothed by repeated Pleistocene glaciation. Scattered mafic intrusives occur as dikes in the lower bay and become more abundant and larger in the upper reaches. The dikes do not seem to be a major factor in geomorphic control. Topographic relief is generally less than 300 feet. Although bedrock outcrops are mostly of broadly rounded granites, jointing, fracturing and glacial quarrying is abundant enough to provide a rugged topography on a local scale of tens of feet (Figures 42, 43). The basic topography is that of preglacial north-south trending stream valleys superimposed on a northwest-southeast trending structural pattern.

A late Pleistocene, Wisconsin glacial till blanket of a few to tens of feet lies over the entire area (Figure 44). Away from the shoreline only scattered outcrops of bedrock occur. Smaller, often en-echelon recessional moraines are abundant in the area of Gouldsboro Bay and are shown in figure 8. These features are responsible for numerous till bluffs and some smaller points within the bay. The Dyer Neck Moraine, which stretches for about five miles from Wyman, south of Milbridge nearly to the shore of Gouldsboro Bay is the largest linear moraine in the area. It appears to be responsible for the shelf-ridge bottom topography of the upper main bay. The Grand Marsh moraine resulted in the blocking and "beheading" of ancient "West Bay" and is the basis for the two-armed shape of modern Gouldsboro Bay.

Along the shore of the bay complex the till blanket has been

Figure 42. Granitic, exposed shore of the outer islands off Gouldsboro Bay. The once continuous forest overlying glacial till is gradually being removed by wave action and sea level rise.

Figure 43 Jointed granitic shore on outer Dyer Neck.

Figure 44. Till bluff being slowly removed by bay wave action.

Figure 45. Sandy-gravelly beach in topographic low area of northwest Gouldsboro Bay.

winnowed by intertidal wave action. The clay, silt and sand sizes have been removed, leaving extensive deposits of cobble and boulder lag lying on bedrock. This process is observable in the lower reaches of West and Joy Bays and becomes more pronounced southward. In topographically lower areas in Gouldsboro Bay, sand and gravel have been deposited by wave action (Figure 45). To a large degree, the location of these pocket beaches is a function of the jointing pattern of the bedrock (i.e., presence of small headlands and bays) and proximity to a sediment source (i.e., a till deposit). In the southern, more exposed areas of the bay, the lag of pebbles, cobbles and boulders lying over bedrock bottom persists subtidally to a depth of 10-15 feet (3-5m). On the outer islands, this type of bottom reaches 40-65 feet (12-20m) before disappearing under a soft bottom of gravelly to silty sand. A detailed geomorphologic study of the Bay is being prepared by Shipp et. al.

During Wisconsin deglaciation, from about 12,000-13,000 years BP, a rapid submergence of the present coast by rising sea level, in front of the retreating ice resulting in the depositation of a blanket of sediment over the till. This sediment of clay, silt and glacial debris is commonly found throughout coastal Maine and has been named the Presumpscot Formation (Bloom, 1963). With the ice removed, rapid upward rebound of the coastal area resulted in re-exposure and a retreat of the shoreline to a position five to ten miles seaward of its present location. Since that time, a slow depression of the crust, accompanied by continued slow sea level rise, has resulted in a general submergence of the coast and a marked "drowned topography" (Figures 2, 46-47).

Based on an older study (Schnitker, 1974), between 11,000 and 8,000 year BP, sea level would have remained virtually constant at about -55m. However, seismic work, bathymetric profiles based on the NOS nautical charts and the apparent lower limit of subaerial erosion features, a depth of -55 to -65m seems more likely (Figure 47). In any case, three thousand years of virtually constant sea level would have been sufficient to produce well-developed shoreline features (exposed bedrock and lag cobble shores, till cliffs, spits, tombolos, and marshes) and define the lower limit of inshore waters. This early Holocene shoreline, besides being the lower limit of abundant irregular topography occurs near the photic limit, and may also be the outer limit for winter lobster migration. Morphologically, the “low-stand” shoreline is extremely important in determining the present distribution of benthic communities, and is a key element in the interpretation of the Pleistocene history and development of the coastline. A continuation of this geomorphological study is being developed as a doctoral dissertation at the University of Maine.

Beginning about 8,000 years BP, flooding of the inshore shelf began, resulting in the immediate development of a drowned

Figure 46. Sea level position, relative to present sea level, over the last 13,000 years.

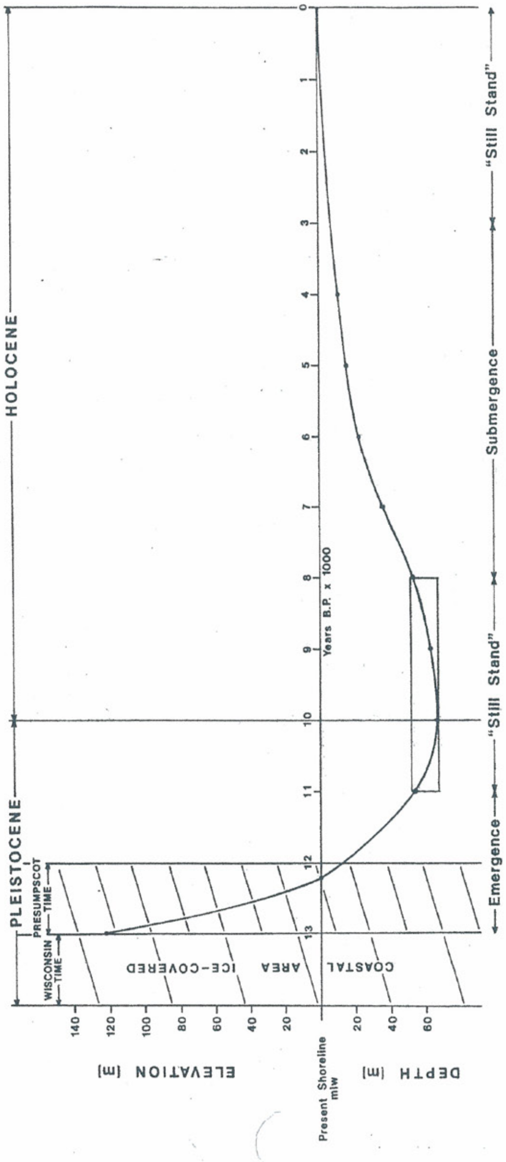
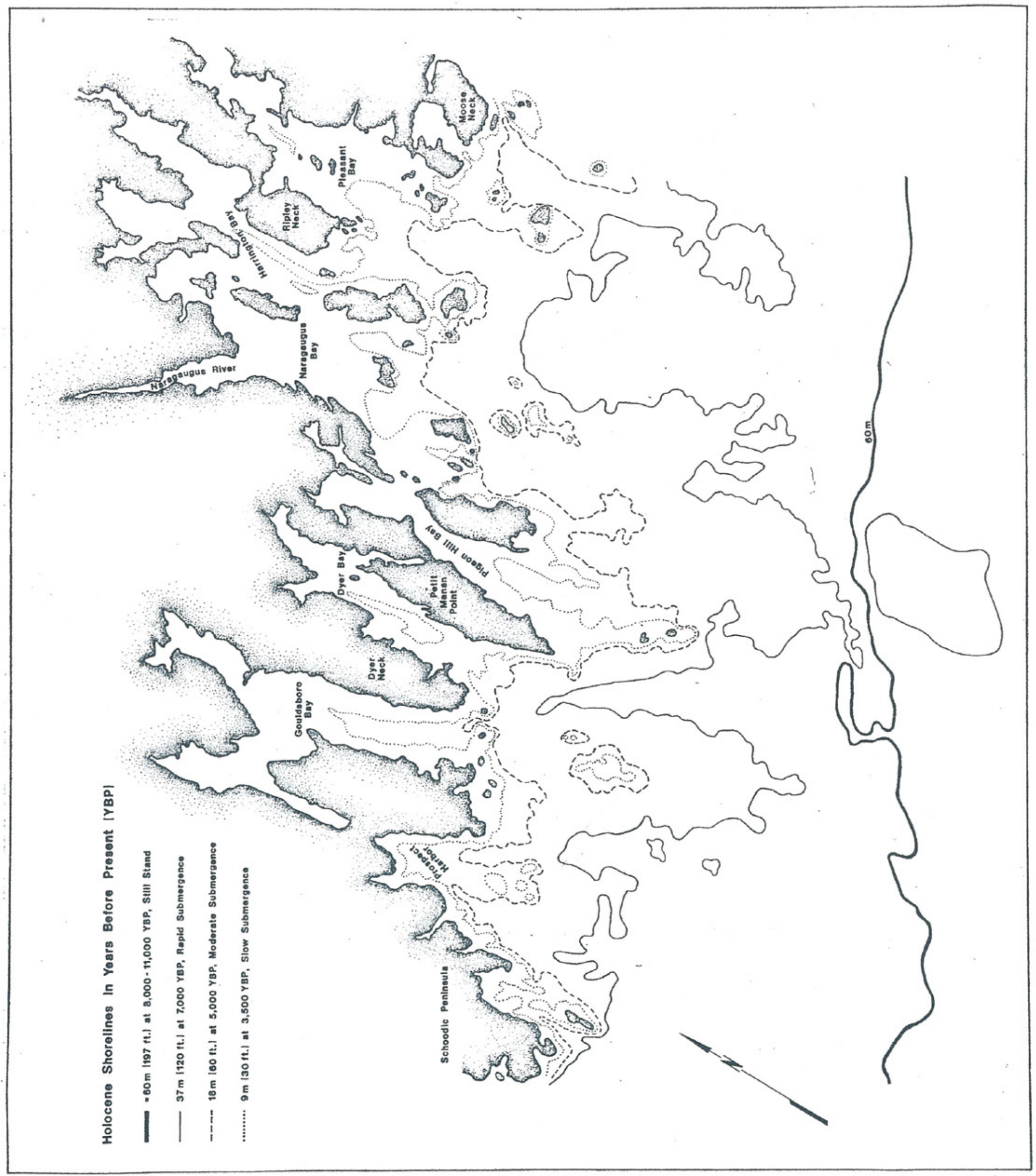


Figure 47. Shorelines of the latest Pleistocene and Holocene In the Gouldsboro Bay area.



topography and the ancient Gouldsboro and Dyer Bay complex.

From about 8,000-6,000 years BP, the present Gouldsboro Bay was a coastal valley and was probably forested during much of that time. Tunk Stream and its tributaries cut a narrow valley through the Presumpscot clay and into the underlying till along much of the length of the bay. About 5,500 years BP, flooding of the lower bay began through the narrow Eastern Way. By about 3,000 years BP, most of the present main bay had been flooded and yet the openings to the open ocean remained narrow. Thus, for a good part of its modern history (approximately 3,000-6,000 years BP), Gouldsboro Bay functioned like Taunton Bay in Hancock County; a marine pond with little shore erosion and with a strong tidal current through its narrow entrance.

In the last few years, sea level rise has continued at a slow rate (Figure 46), and at the same time the bay has become more and more open to the effects of open ocean waves. Shoreline erosion of the unconsolidated intertidal deposits progressed into the main bay as silt-sized material removed by wave action became deposited in the upper arms of the bay as mud flats. In small basins scattered along the uppermost reaches of the bay and particularly in the southern part of Grand Marsh Bay, fresh water marshes had developed during the early Holocene. Upon flooding by the rising sea between 2,000 and 3,500 year BP, these areas developed salt marsh communities (Figures 30, 31). The baffling effect of the salt marsh grasses provided for rapid accumulation of silts eroded from the lower bay and subsequent building of marsh surface at the same rates as sea level rise. Later, numerous narrow fringing marshes developed along more protected shores in the upper sections of the bay (Figure 49).

Figures 50-53 show the relationship of the present marine sediments and the later Pleistocene Presumpscot Formation to the underlying till and bedrock. The Presumpscot Formation serves as an excellent marker horizon and for all practical purposes can be used as a boundary between Pleistocene and Holocene. While it may be thin or absent over the bedrock ridge lying on either side of Gouldsboro Bay, it is quite consistent beneath the bay and along the shore, wherever it has not been removed by erosion during the past few thousand years. Its frequent absence along the ridges may result from a lack of original deposition (due to higher wave energies on the shallower ridges), from erosion during re-exposure of the shore (13,000-12,000 BP), from recent erosion or re-working by vegetation, or from some combination of all three.

Per nautical mile, the relief on the Dyer Bay, Gouldsboro Bay ridges is 60-120 feet. In the central parts of the bay, the same relief per mile is about 40-60 feet (Figure 8). Assuming that the continental glaciation had provided a surface of more or less equal relief on the ridges and in the valleys, and that the cover of ground moraine in the two areas is nearly equivalent, the difference in relief suggests considerable post-glacial

Figure 48. Inner end of the Grand Marsh showing retreating forest.

Figure 49. Fringing marsh along the border of a mud flat.

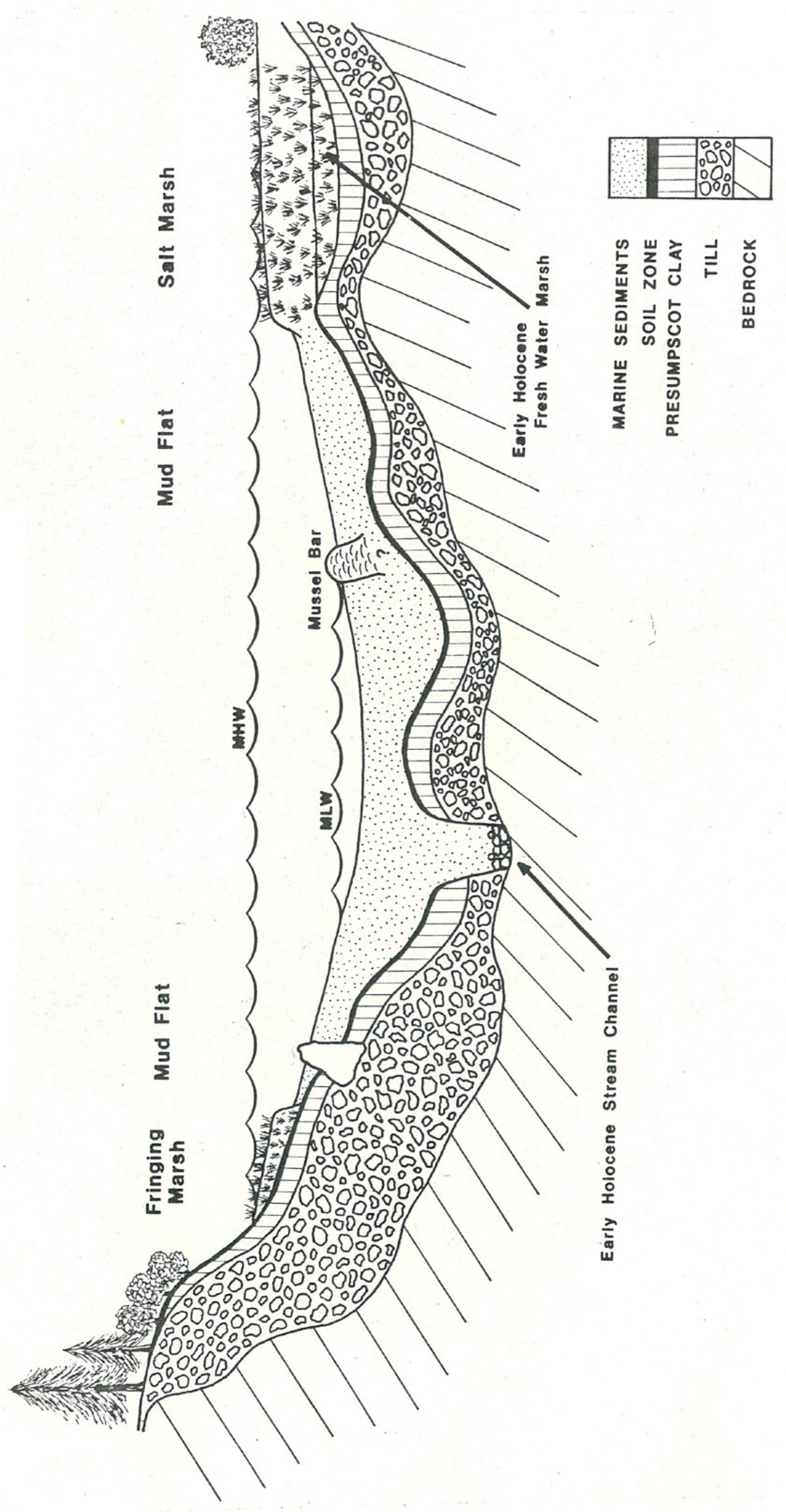


Figure 50. Section across of upper bay showing sub-bottom stratigraphy.

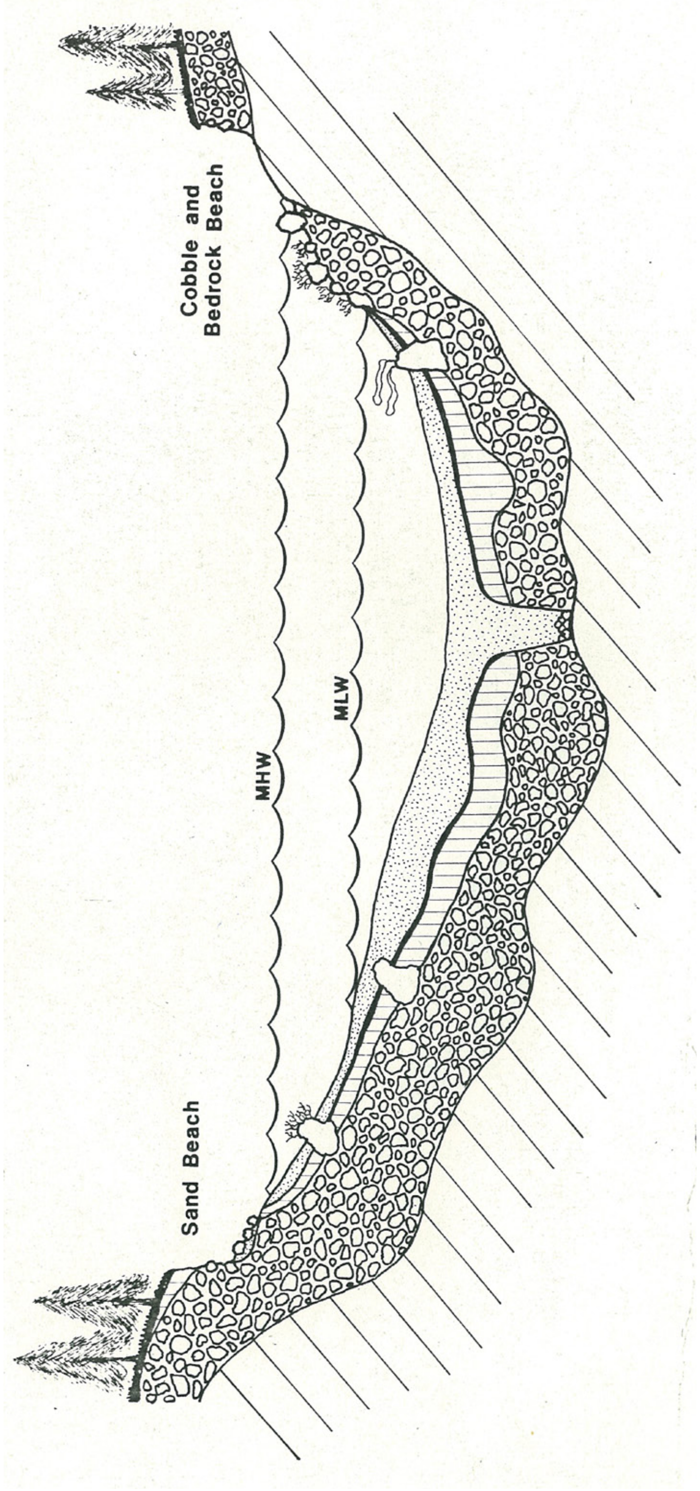


Figure 51. Section across bid bay showing sub-bottom stratigraphy.

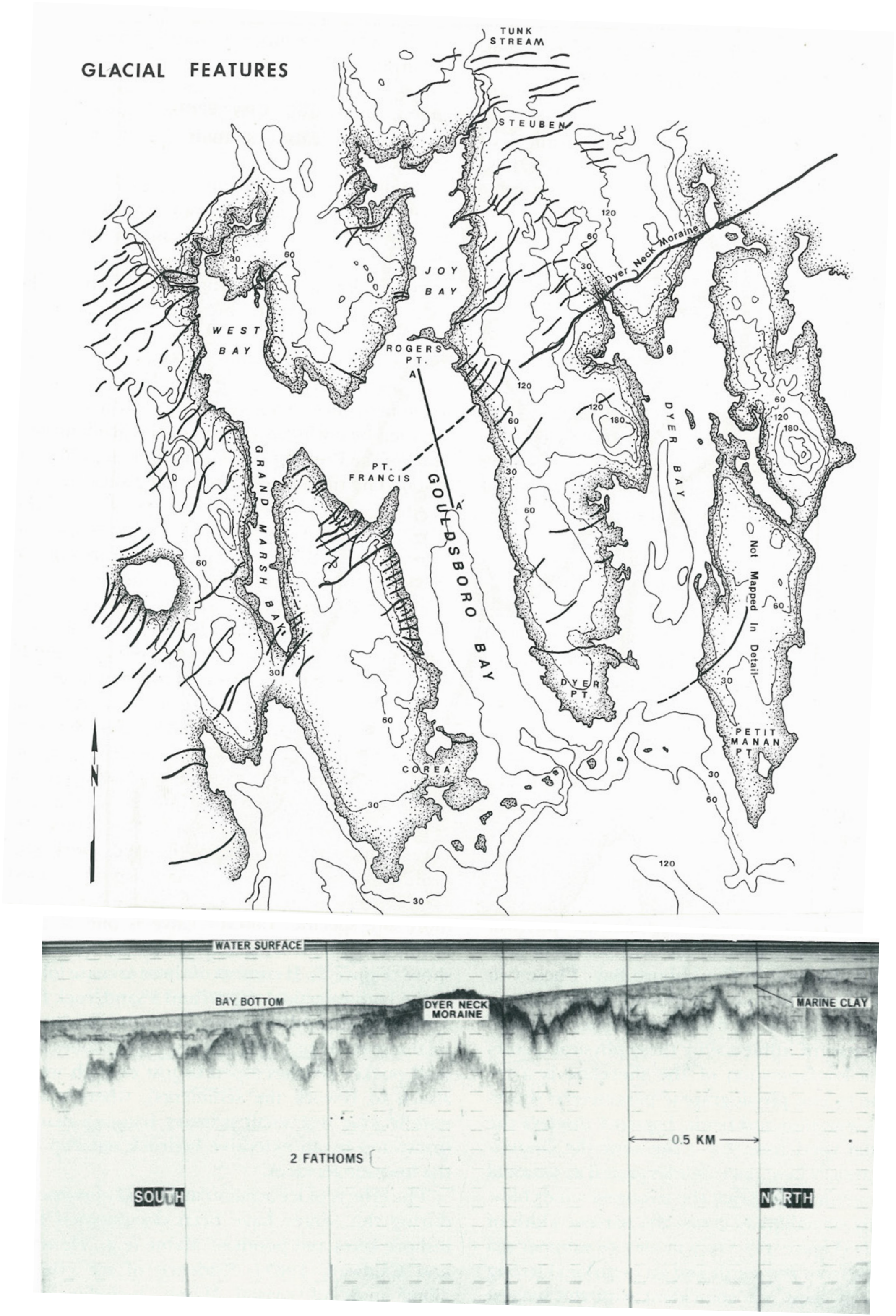


Figure 52 Longitudinal (N-S) sub-bottom seismic profile from the upper part of the main stem of Gouldsboro Bay showing the extensive layer of marine clay (the Presumpscot Formation) laid down at 12-13,000 yrs. BP.

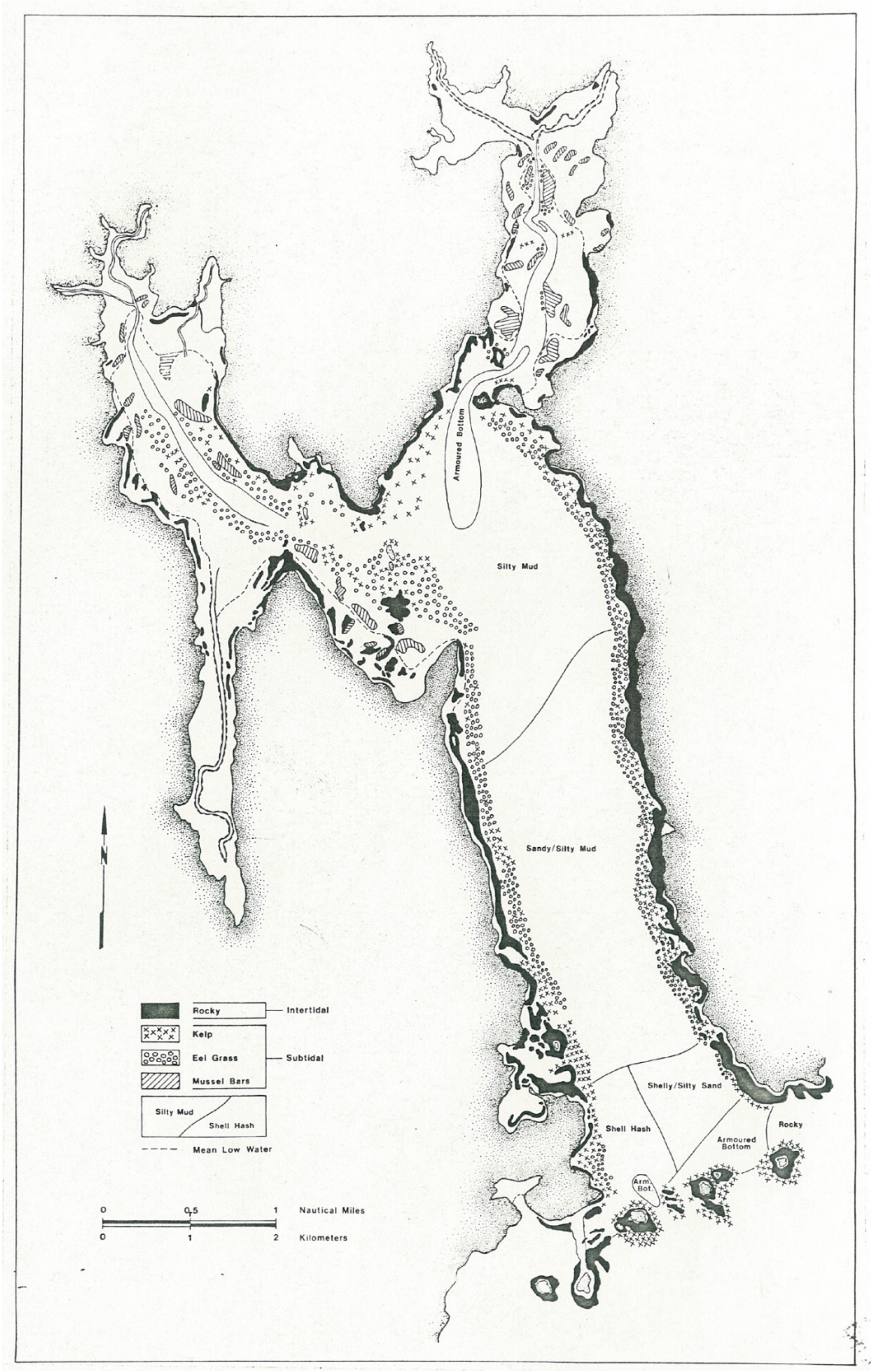


Figure 53. Aerial extent of the biological communities of Gouldsboro Bay.

infilling and smoothing by sedimentation. This smoothing, on the order of 20-40 feet, has apparently been accomplished in part by removal of Presumpscot clay from the ridges during the rapid emergence and deposition in the bays. Subsequent erosion of the ridges with deposition of marine sediments in the bay has continued this process. The difference in relief, the seismic profiles, and the cores all indicate that 20-40 feet of post glacial sediments, including Presumpscot clay, a soil or peat zone, and dominantly silty marine sediments, are present in the central part of the Bay.

The nature and distribution of biological communities are largely determined by the character of the substrate; this characterization is listed below in table 1 and shown in figure 53. Sediment character in terms of grain size and percentage composition of organic and mineral components is presently being analyzed and will be treated in detail in a later report. The most striking character of the preliminary analyses is the regular and consistent increase of organic percentage in the bottom sediments from values of less than 2% near the mouth to over 10% on parts of the flats at the head of the bay. Primary production is limited on the flats, and the source of these organics must come from further down the bay, either as plankton and/or macro-algal detritus. Since the latter is by far the dominant source of organics within the bay (Figure 90), it seems likely that rockweed is the primary source and that there is a hydrographic mechanism forcing the fine organic detritus to the head of the bay and depositing it on the flats.

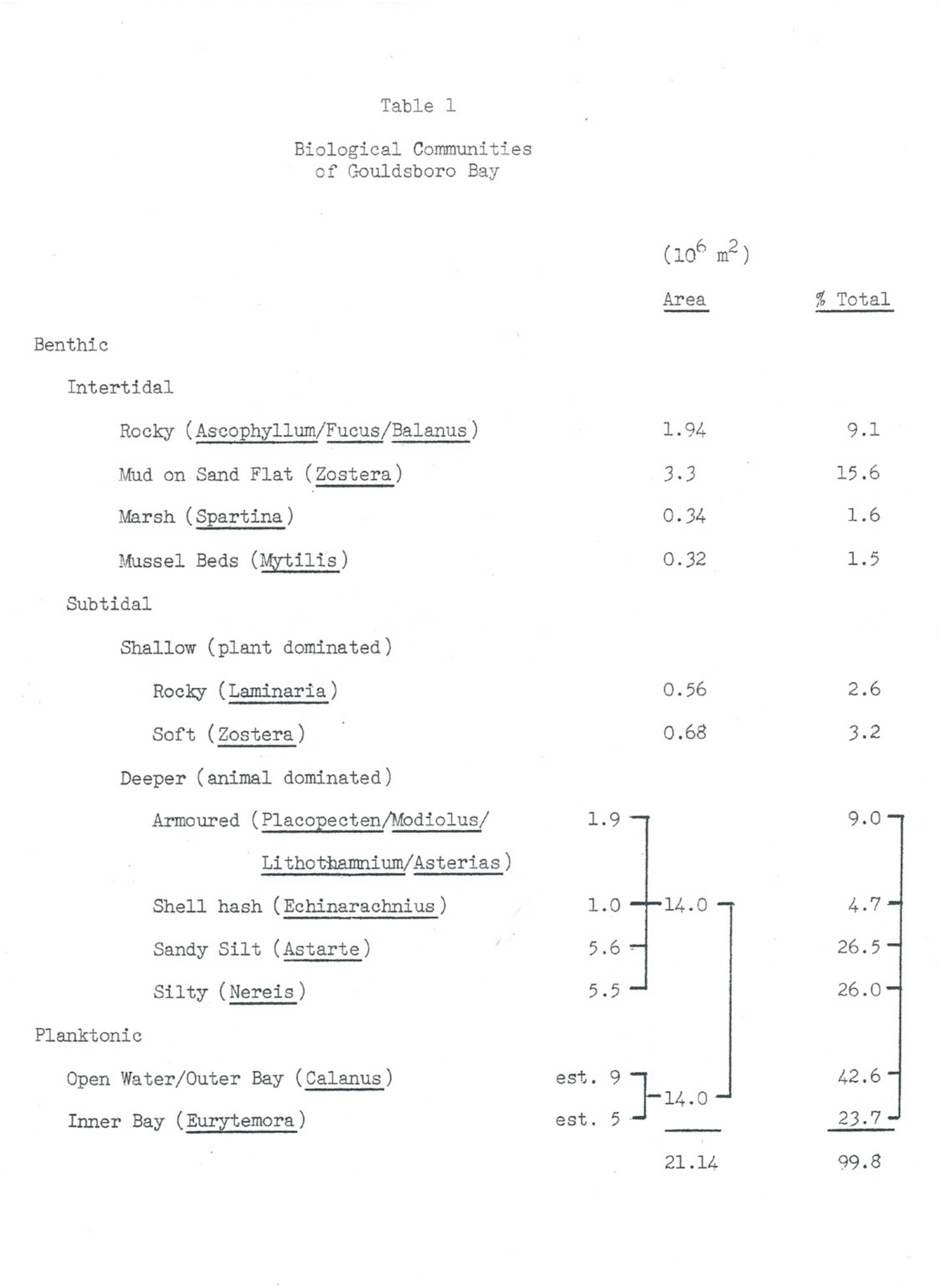


Table 1

Biological Communities
of Gouldsboro Bay

	(10^6 m^2) Area		% Total
Benthic			
Intertidal			
Rocky (*Ascophyllum*/*Fucus*/*Balanus*)	1.94		9.1
Mud on Sand Flat (*Zostera*)	3.3		15.6
Marsh (*Spartina*)	0.34		1.6
Mussel Beds (*Mytilis*)	0.32		1.5
Subtidal			
Shallow (plant dominated)			
Rocky (*Laminaria*)	0.56		2.6
Soft (*Zostera*)	0.68		3.2
Deeper (animal dominated)			
Armoured (*Placopecten*/*Modiolus*/*Lithothamnium*/*Asterias*)	1.9		9.0
Shell hash (*Echinarachnius*)	1.0	14.0	4.7
Sandy Silt (*Astarte*)	5.6		26.5
Silty (*Nereis*)	5.5		26.0
Planktonic			
Open Water/Outer Bay (*Calanus*)	est. 9	14.0	42.6
Inner Bay (*Eurytemora*)	est. 5		23.7
		21.14	99.8

HYDROLOGY

The tides in Gouldsboro Bay are semi-diurnal and display a moderate diurnal inequality (up to 0.4m). Mean tidal range at the entrance of the bay is approximately 3.2 meters and spring tides may exceed 4 meters. The regular geometry of Gouldsboro Bay is significant in determining characteristics of the tidal wave.

In plan view (Figure 8), Gouldsboro Bay proper is rectangular and width remains nearly constant along the axis. West Bay and Joy Bay are shallow, irregular extensions of Gouldsboro Bay, but combined they include less than 10% of the total volume of the system. The cross section of Gouldsboro Bay is sub-rectangular along the seaward half. Here, depth decreases headward in a gradual and linear manner. In the upper half of the Bay, the cross-section becomes more V-shaped and depth decreases abruptly from 11 to 5 meters (MLW) between 4 and 5 kms headward of the mouth.

Predicted and measured tidal range at the head of Gouldsboro Bay correspond closely with predicted range at the mouth. Amplification of the tidal wave due to geometry effects and alternation from frictional energy dissipation are minimal and approximately in balance. This is typical of deep and geometrically regular bays along the Maine coast. Tidal shore relationships along Gouldsboro Bay indicated that the tidal wave is largely a standing wave-type. High water at the headward end is only 15° out of phase (three minutes later) with high water at the mouth. Maximum tidal currents are therefore 90° out of phase with tide-level fluctuation, occurring approximately at mid-tide.

Total water volume in Gouldsboro Bay at mean tide-level is approximately $1.9 \times 10^8 m^3$. The mean tidal prism is $5.2 \times 10^7 m^3$ or approximately 27% of the bay volume. Maximum tidal prism at spring tide is $6.5 \times 10^7 m^2$ and approaches 35% of the bay volume. Mean tidal discharge is approximately $1200 m^2/s$. Discharge at maximum ebb and flood exceeds $3000 m^2/s$ Local tidal velocities may reach 80cm/s near the surface and 20cm/s near the bottom at maximum tidal flow.

Several small, freshwater streams enter the Gouldsboro Bay system at the headward end in Joy Bay and West Bay. Freshwater influx from these streams is very small compared with tidal discharge however. Flow measurements taken in the early fall indicated that combined freshwater flow of all streams did not exceed $5 m^3/s$. Gouldsboro Bay is therefore tide dominated and generally well mixed. This is reflected in a high dispersion coefficient based on the mean tidal prism, an average bay cross section and freshwater discharge of $5 m^3/s$ is approximately $1.2 m^2/s$. Assuming a mean bay volume of $1.9 \times 10^8 m^3$, and a mean rate of freshwater influx, the flushing time is approximately 32 days. Actual flushing time probably varies between 15 and 60 days depending on tidal range and variations on freshwater supply. Also, storm effects on circulation, mixing and flushing are probably significant, but have not yet been examined.

Despite strong tidal effects and low freshwater influx, weak vertical and longitudinal salinity gradients persist in Gouldsboro Bay (Figure 54). An intensive two week survey of salinity and temperature structure in the bay from neap to spring tide shows a slowly varying system. Weakest vertical stratification (0.1 to 0.4ppt) occurs near the mouth of the bay (Figures 54a, 55a). The largest vertical gradients occur along the headward third of the bay and range from 0.4 to nearly 1ppt. Temperature distribution closely parallels salinity structure (Figures 54b, 55b).

In general, Gouldsboro Bay is laterally well-mixed (Figures 56, 57), but lateral salinity distribution shows a significant feature. Salinity near the mouth of the bay is consistently greater on the east side. This could be due to a Coriolis effect; however, it is more likely due to a weak tidal pumping system through the restricted by entrance. Intertidal effects at the multiple entrance may cause one or more inlets to be either flood or ebb dominated.

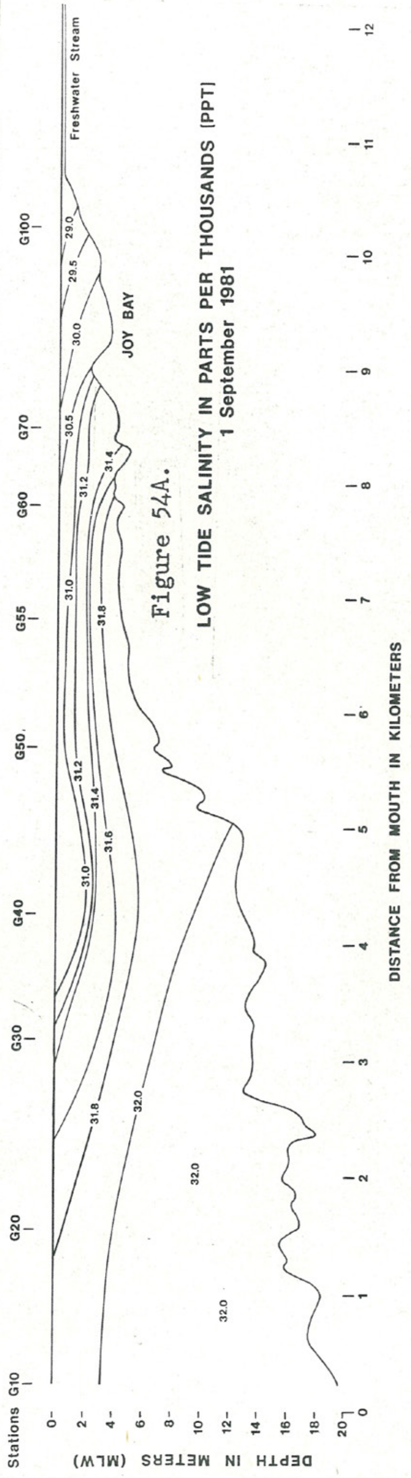


Figure 54A. LOW TIDE SALINITY IN PARTS PER THOUSANDS (PPT) 1 September 1981

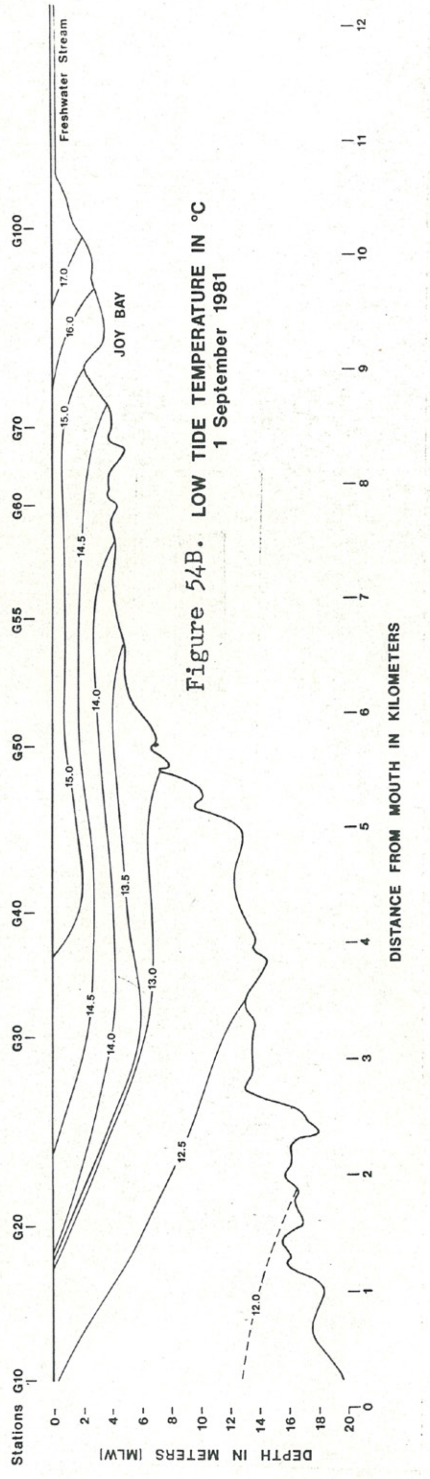


Figure 54B. LOW TIDE TEMPERATURE IN °C 1 September 1981

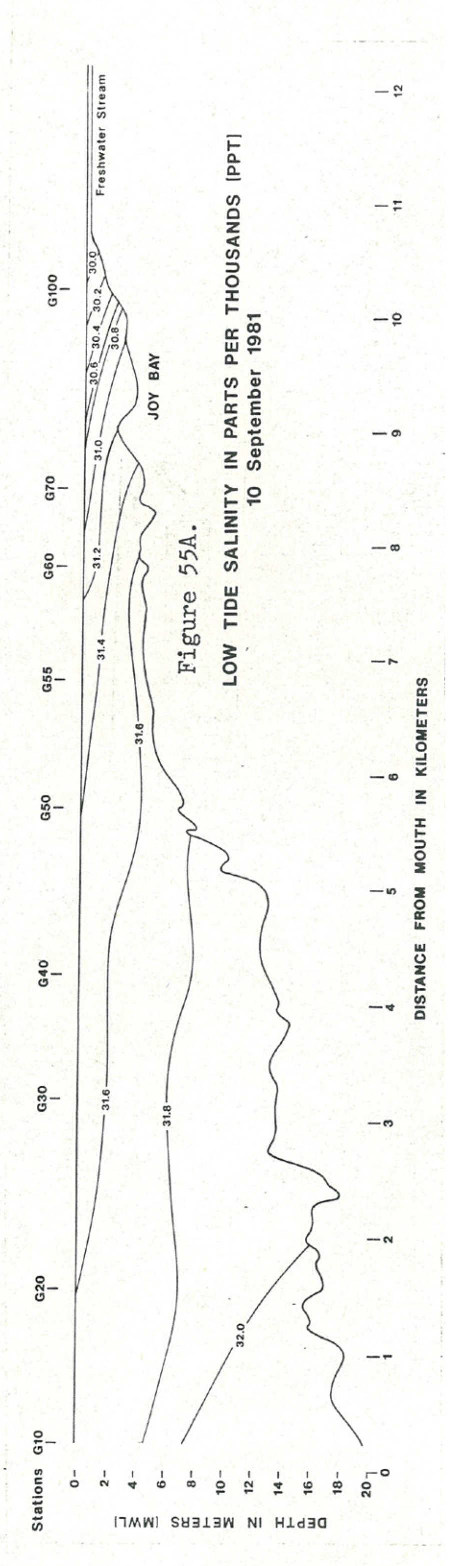


Figure 55A.

LOW TIDE SALINITY IN PARTS PER THOUSANDS [PPT]
10 September 1981

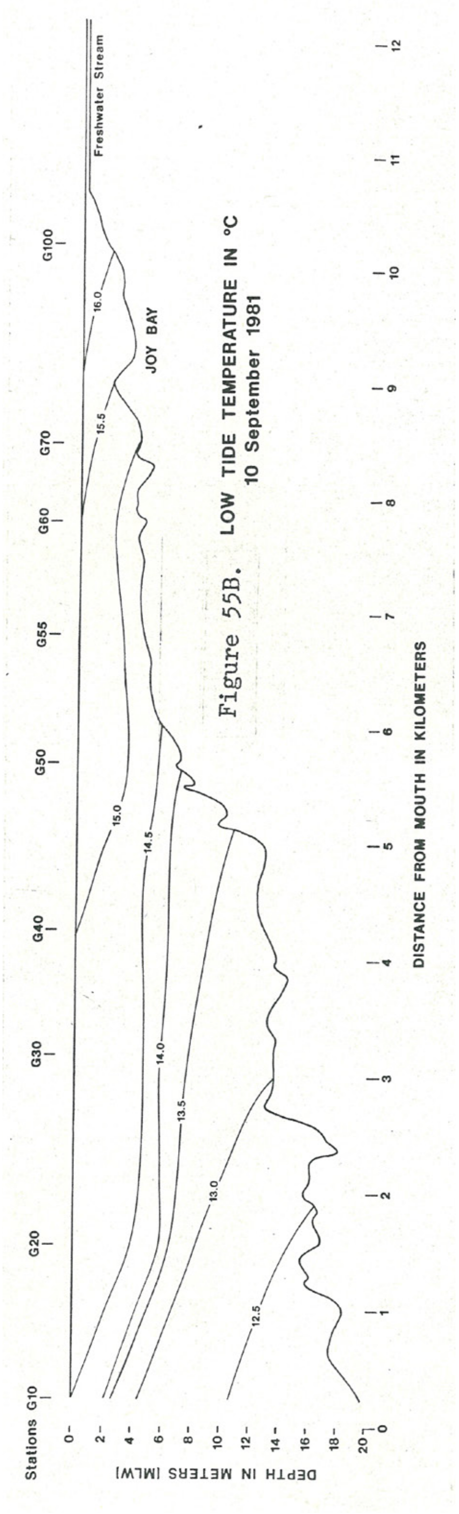


Figure 55B.

LOW TIDE TEMPERATURE IN °C
10 September 1981

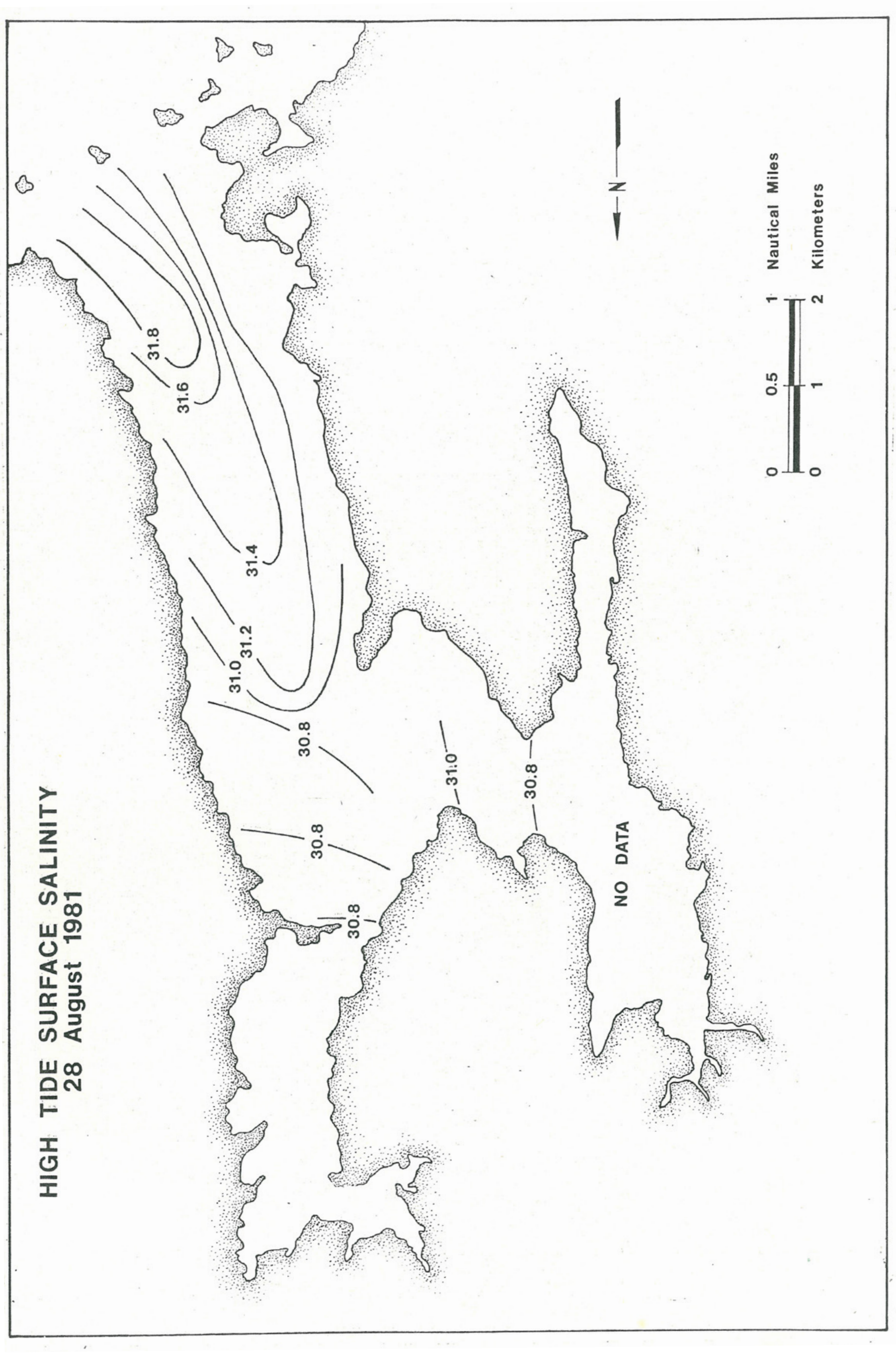

HIGH TIDE SURFACE SALINITY
28 August 1981
31.8
31.6
31.4
31.2
31.0
30.8
31.0
30.8
30.8
30.8
NO DATA
N
0
0.5
1
Nautical Miles
0
1
2
Kilometers

Figure 56.

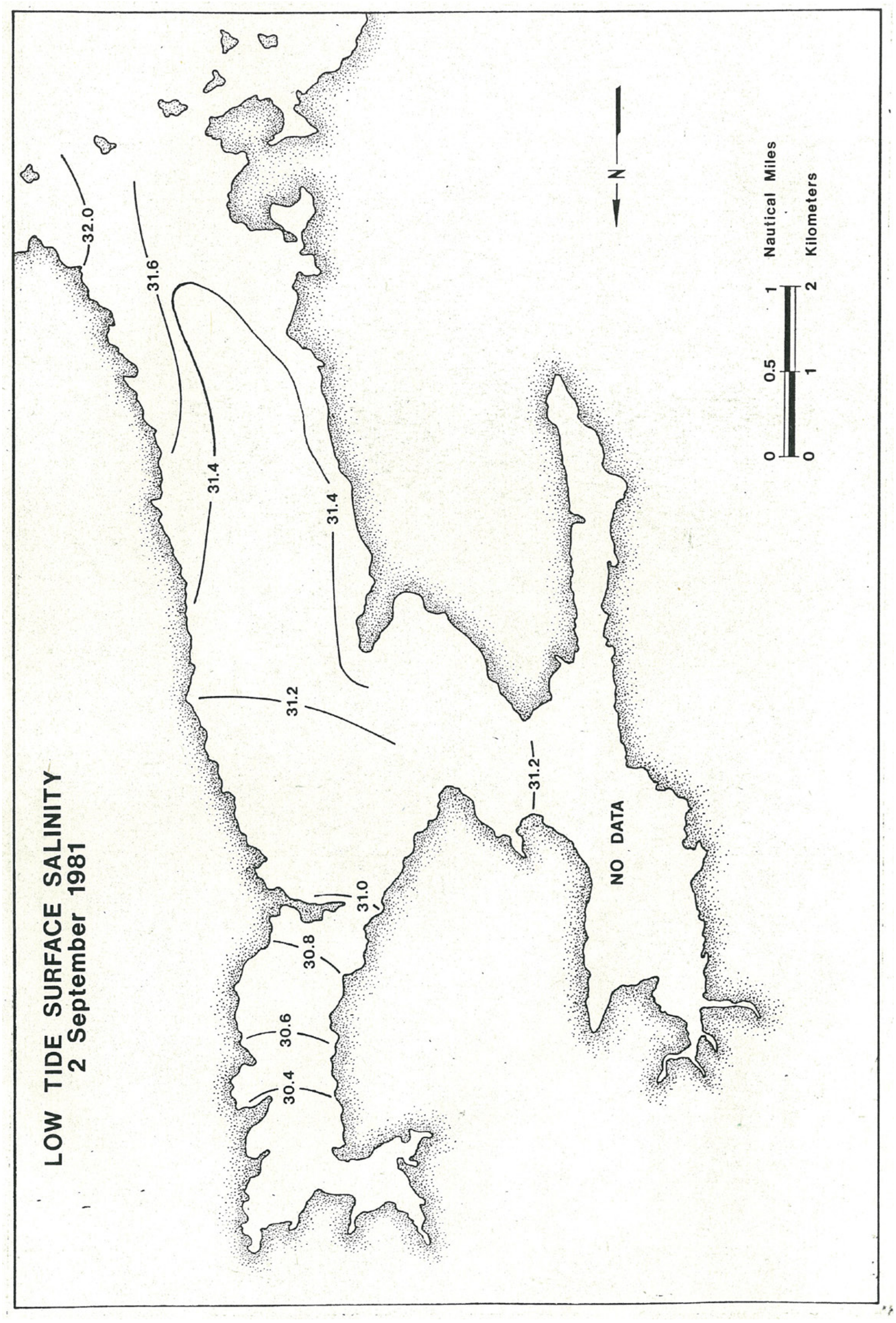

LOW TIDE SURFACE SALINITY
2 September 1981
32.0
31.6
31.4
31.4
31.2
31.2
31.0
30.8
30.6
30.4
NO DATA
N
0
0.5
1
Nautical Miles
0
1
2
Kilometers

Figure 57.

BIOLOGICAL COMMUNITIES

A characterization of the biological communities of Gouldsboro Bay is shown on figure 53 and outlined in table 1.

Benthic studies of rock bottoms were carried out with 1/16m^2 quadrants at high (2-3m mlw), mid (0.5-1m mlw), and low (-1 to 0m mlw) tide levels and in the subtidal at 2.5, 5 and 10m below mean low water. Station locations are shown in figure 19. Generally, 16 quadrats were thrown per station/depth level, although as few as six and as many as 28 were used at some sites.

All of the dominant macroalgae and invertebrates were tabulated, along with biomass at each site. Also, by a variety of means, discussed below, primary productivity in terms of biomass increase for the benthos and C^{14} for the plankton was determined. The emphasis of this report is on primary productivity. Although a wide range of algae and invertebrates are briefly discussed, our treatment centers on the dominant benthic primary producers *Ascophyllum nodosum* (rockweed), *Laminaria saccharina* and *Laminaria longicuris* (kelp) and *Zostera marina* (eel grass).

Intertidal

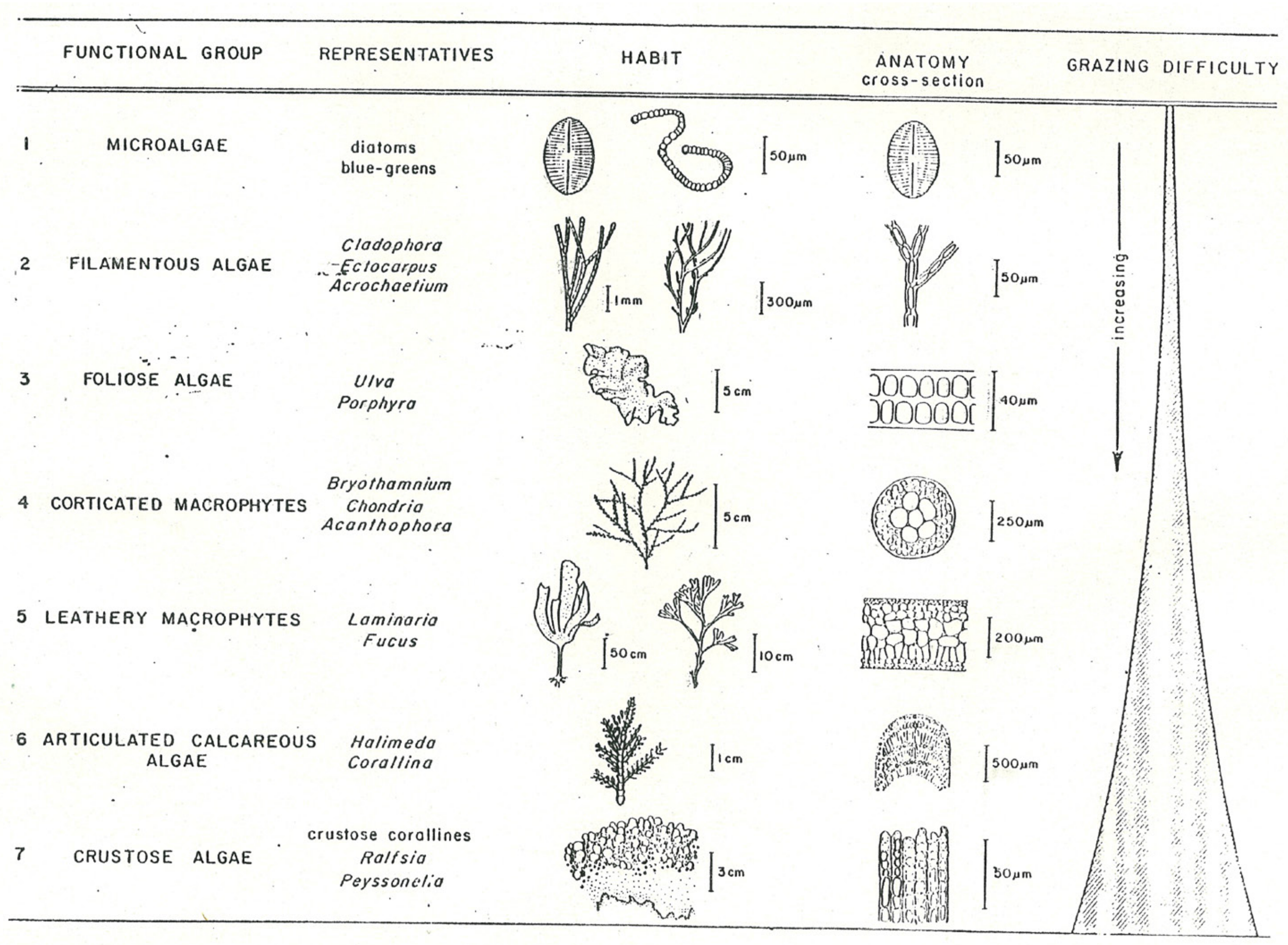
Rocky Intertidal

The rocky, algal covered intertidal shore is a primary feature of Gouldsboro Bay, as well as much of the Maine shoreline (Figures 53, 58, 59). Generally, the proportion of soft bottom increases from the outer areas to the inner, more protected reaches. Nevertheless, it is only in the upper arms, Joy Bay and West Bay, that the rocky intertidal is largely replaced by marshes and mud flats. Aerially, the rocky intertidal occupies only about 10% of the total surface of the bay. However, its high level of primary productivity (over 60% of the total for the bay) makes it the most important single community in terms of total bay function.

Ten intertidal stations were extensively sampled on the shores of Gouldsboro Bay. Those stations were grouped into four regions of the bay from its outer to inner reaches (Figure 19), and at each station lower, middle and upper intertidal were sampled with 1/16m^2 quadrants. The patterns of biomass and demography of the dominant primary producers and the macro invertebrates were determined from those samples. Tables 2 & 3 show the algal community structure in terms of algal groups, or habitat forms, and the distribution of biomass within those groups. As can be seen from the table, the biomass is concentrated in algal group 5, the leathery macrophytes. Within the bay intertidal, the rockweed *Ascophyllum nodosum* heavily

Figure 58. Rocky intertidal of the eastern shore of Gouldsboro Bay.

Figure 59. Area shown in figure 58 from the water. Note the extensive rock weed cover.



	FUNCTIONAL GROUP	REPRESENTATIVES	HABIT	ANATOMY cross-section	GRAZING DIFFICULTY
1	MICROALGAE	diatoms blue-greens	50µm	50µm	increasing
2	FILAMENTOUS ALGAE	*Cladophora* *Ectocarpus* *Acrochaetium*	1mm 300µm	50µm	
3	FOLIOSE ALGAE	*Ulva* *Porphyra*	5 cm	40µm	
4	CORTICATED MACROPHYTES	*Bryothamnium* *Chondria* *Acanthophora*	5 cm	250µm	
5	LEATHERY MACROPHYTES	*Laminaria* *Fucus*	50 cm 10 cm	200µm	
6	ARTICULATED CALCAREOUS ALGAE	*Halimeda* *Corallina*	1 cm	500µm	
7	CRUSTOSE ALGAE	crustose corallines *Ralfsia* *Peyssonelia*	3 cm	50µm	

Table 2. Algal functional groups as used in benthic analysis.

Table 3. Algal biomass (g-wet/m2) of the hard bottom communities of Gouldsboro Bay.

		Intertidal																								
Depth		High		Middle					Low						2.5m				5m				10m			
Algal Groups		3	5	1,2	3	4	5	6,7	1,2	3	4	5	6	7	1,2	3,4	5	7	1,2	3,4	5	7	1,2	3,4	5	7
Bay Location	Sta																									
Outer	7			145	145	280	13,420	0	167	1926	3098	3182	58	2	31	73	10,323	16	285	2136	11,819	40	72	54	142	120
	8		ND	112	136	551	11,651	0	41	118	2265	5067	7	1	37	86	12,144	16	224	448	10,528	118	33	8	210	118
	x			128	140	416	12,536	0	104	1022	2672	4124	32	1.5	34	80	11,233	16	255	1292	11,174	79	52	31	176	119
	sum					16,965					4955.6					11,363				≈1213						
Mid-Outer	11			4.3	0	91	22,605	0	51	0	1020	11,606	0	25	420	2280	3300	86								
	25		ND	3.3	0	98	10,841	0.9	37	0	745	12,849	12	49	183	527	1582	144	2	9	207	96				
	23			56	0	203	24,524	23	14	0	434	15,609	0	11												
	x			21.2	0	131	19,323	81	34	0	733	13,355	4	28	302	1404	2441	115	2	9	207	96				
	sum					19,483					14,151					4262				310						
Mid-Inner	13		ND	129		47	38,760	0	0	0	198	13,990	0	17												
	21		14,560	36		195	24,574	0	11		415	16,190	0	1												
	x			82		121	31,667	0	6	0	306	15,094	0	9												
	sum		14,560			31,870					15,415															
Inner	15	285	8117	0		68	50,514	0	7		288	21,867	1	20												
	19	2300	8627	24		84	68,313	0	7		31	20,159	0	0												
	17	0	31,760	61		197	34,898	18	9		376	23,473	0	54												
	x	1185	16,168	42		116	51,242	6	8		232	21,833	.3	25												
	sum		17,363			51,624					22,098															

dominates this group in terms of biomass (Table 3; Figure 61), and it is the biomass and demography of this algae that we will concentrate on in this report.

The age and biomass of *Ascophyllum* steadily increases up the bay (Figure 60; Table 4). In addition, *Ascophyllum* productivity, as measured by weight increase of growing tips, also markedly increases up the bay (Figure 60). In general, the trend in growth from the outer to the inner regions of the bay was one of a reduced number of growing tips per unit area of substratum but an increase in growth rate per tip. The number of tips per/kg also decreases moving up the bay. The rate of biomass accumulation for the summer increases up the bay, as does the net annual biomass accumulation. The latter increased more slowly than the former.

The trend in productivity increasing up the bay is unexpected since both water motion and light penetration (turbidity) decrease in that direction. Also, both phytoplankton productivity and subtidal benthic productivity decrease from outside to the inner reaches of the bay. It is likely that the "inverse" pattern we see is more the result of disturbance than it is a true productivity gradient.

Constant wave induced disturbance, including loss of plant parts, is considerably more important on the outer portion of the bay than it is in the more protected areas. The breaks tend to occur on the distal portions of the plant which facilitates

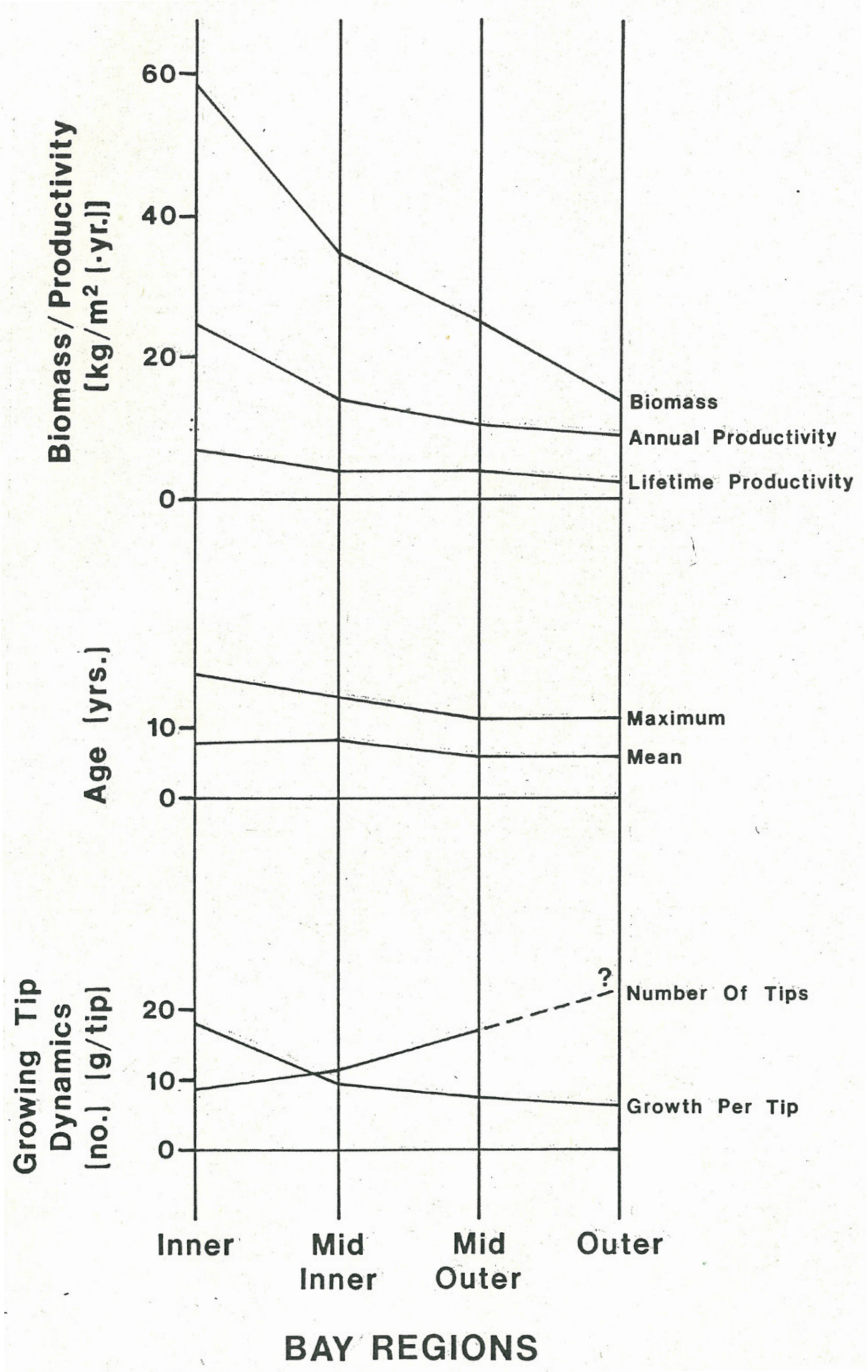


Figure 60. Biomass and productivity (harvest) of Ascophyllum nodosum in Gouldsboro Bay.

Table 4. Demography of Ascophyllum nodosum in Gouldsboro Bay, Maine. Mid-intertidal zones (elongation of blades)

	A	B	C	D	E	F	G	H	I	J
Regions (stations)	Biomass (kg/m^2)	Age (yrs) max	mean	Growing tips (No./m^2)	Growth per tip (g/yr)	Annual Prod. (ExD) (kg)	Annual Prod. (Direct Weight) (kg)	Tips per biomass (No./kg)	Prod. per biomass (G/A) (kg/kg·yr)	Amount of total biomass Ascophyllum (%)
Outer (7,8)	12.5	12	6.2	ND	0.72	ND	9.8	ND	0.78	73.7
Mid Outer (11,23,25)	19	11.7	6.0	17,008	0.8	13.6	13.0	667	0.68	97.5
Mid Inner (13,21)	32	15	8.2	12,032	1.04	12.5	13.2	349	0.41	99.4
Inner (15,17,19)	51	15.3	8.2	10,096	1.8	18.2	22.8	173	0.44	99.3

Figure 61. Rock weed coverage in the rocky intertidal. Most of the light, yellow to dark green plant material is Ascophyllum. The darker, more textured material in the foreground is Fucus.

Figure 62. Abundant littorinid snails on Chondrus crispus bed at low water spring tide in the outer part of Gouldsboro Bay.

branching as they heal their wounds. This probably causes the increased number of tips per quadrat and the increased number of tips per unit biomass. Experimental study is desirable to establish this working hypothesis.

Ascophyllum plants live longer in the inner reaches of the bay. As a result, they grow to a larger size. Since all of the surface of the plant is photosynthetic, and little increase in girth occurs, increased size provides proportionally lower productivity per unit biomass (i.e., a four times increase in biomass only doubles the total productivity - Table 4). Thus, the complex growth form and shape of *Ascophyllum* is well-suited for maximizing the productivity potential of the intertidal in quite water. Unlike the kelps, it is not capable of handling intense wave action as it grows to larger sizes.

Wave induced disturbance decreases up the bay, but herbivore abundance, size and diversity increases, probably as a result of reduced wave action. However, herbivore abundance, size and diversity are somewhat misleading in that the most abundant herbivores in the intertidal (*Littorina littorea*) are incapable of grazing *Ascophyllum. Littorina littorea* is effective at removing fouling epiphytes, including micro, filamentous and leafy functional groups of algae. In effect, the herbivores reduce interspecific competition from fouling algae which may additionally contribute to the increased productivity of *Ascophyllum* towards the inner reaches of the bay.

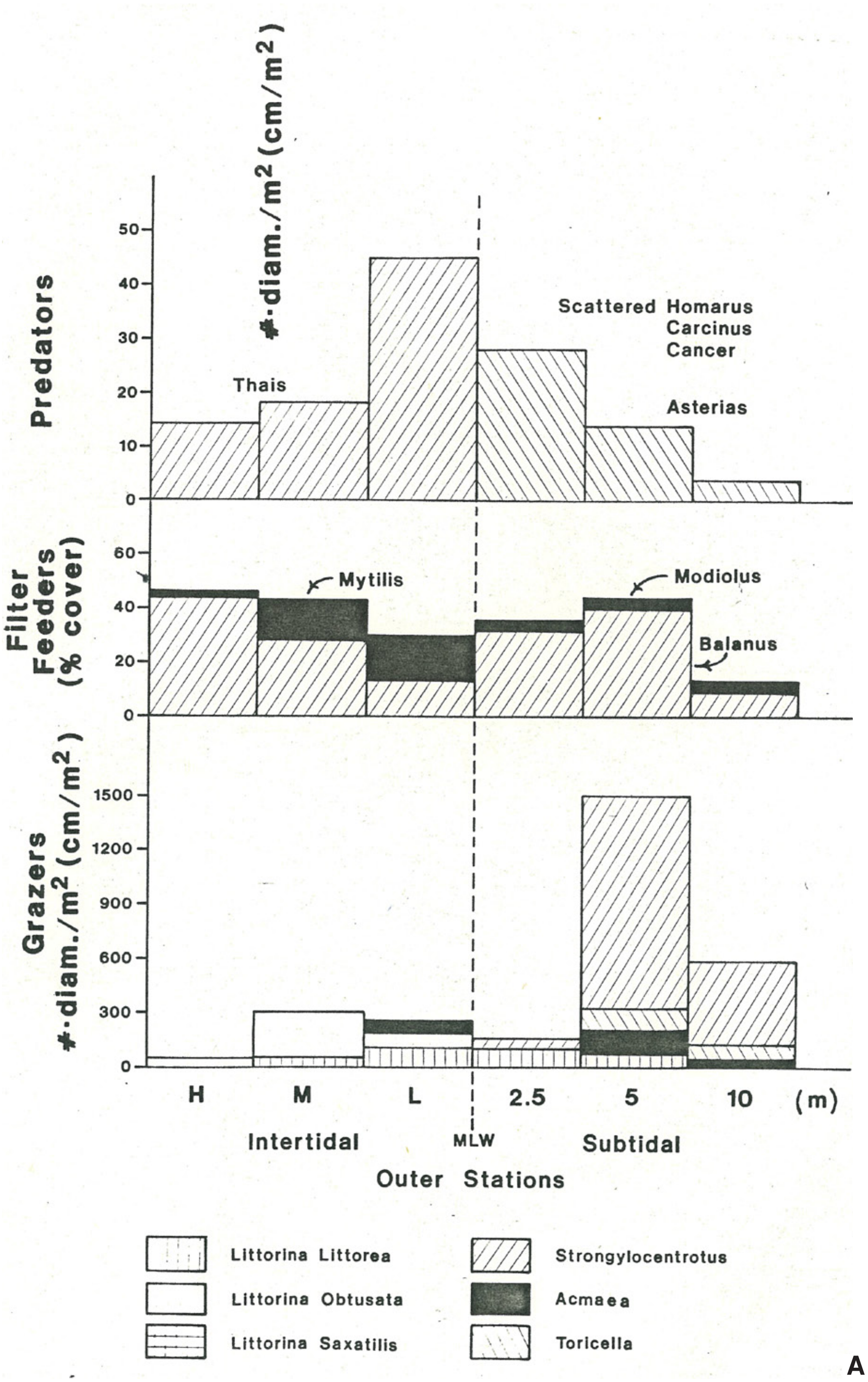
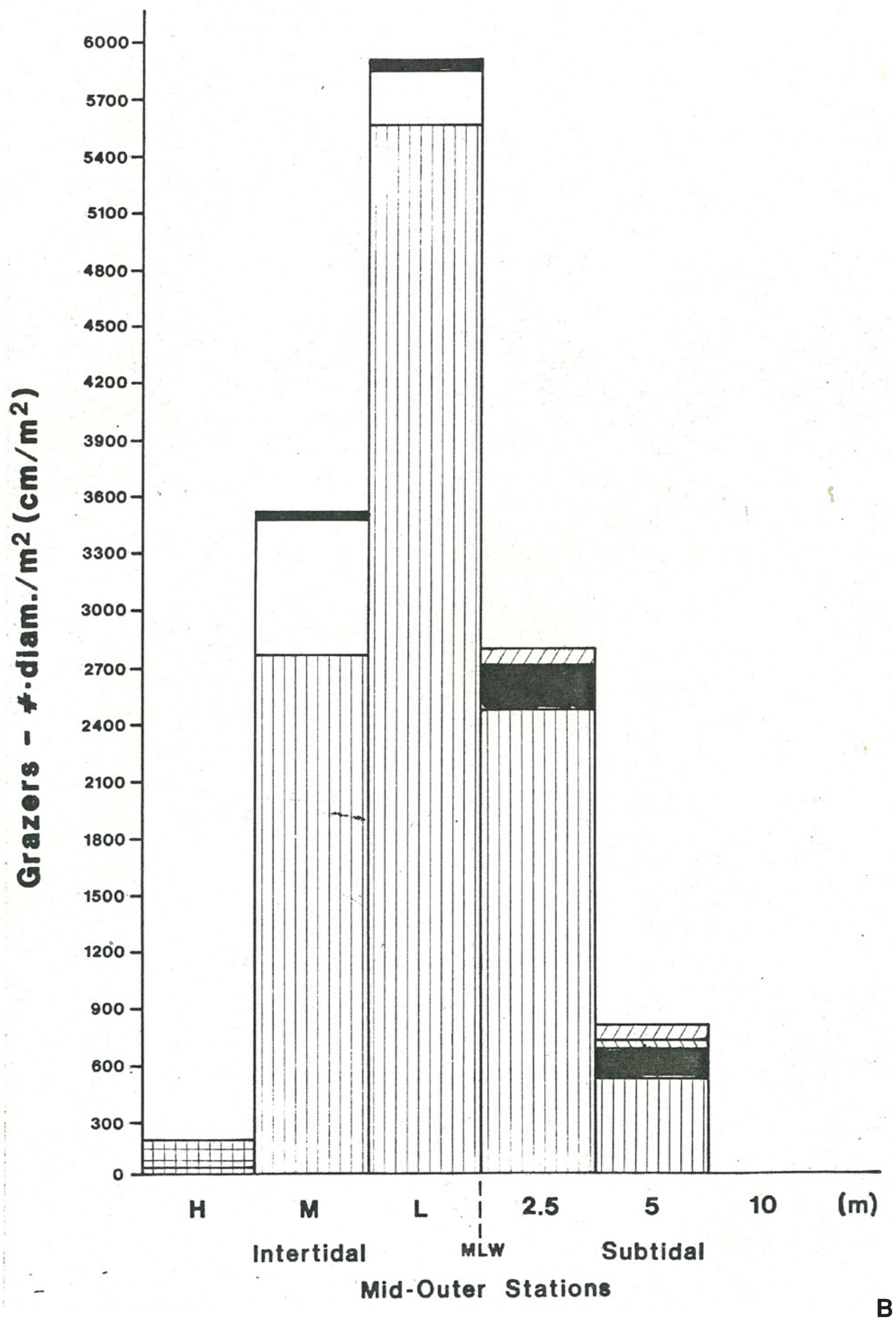


Figure 63A-D. Invertebrate populations, rocky intertidal and subtidal of Gouldsboro Bay.



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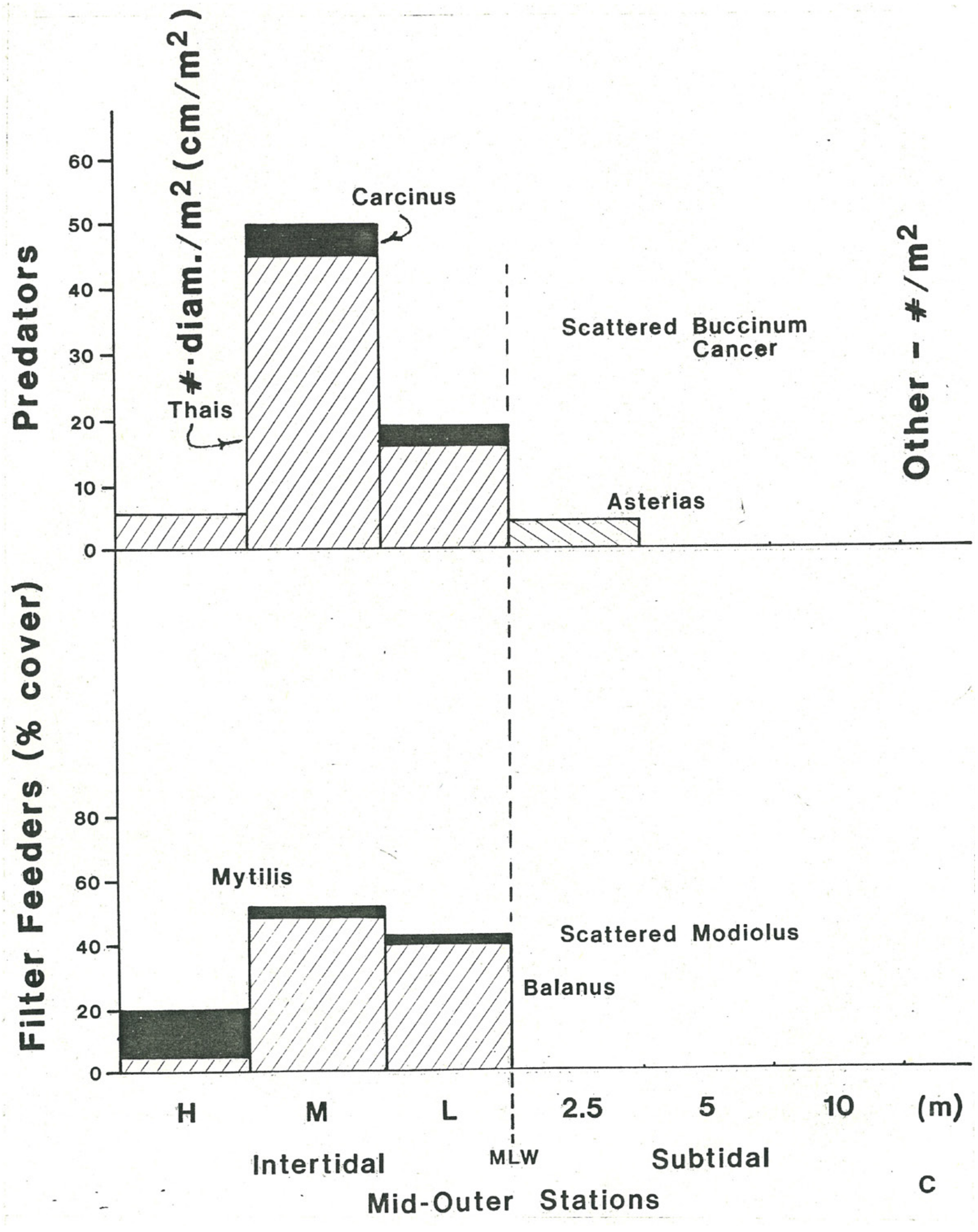

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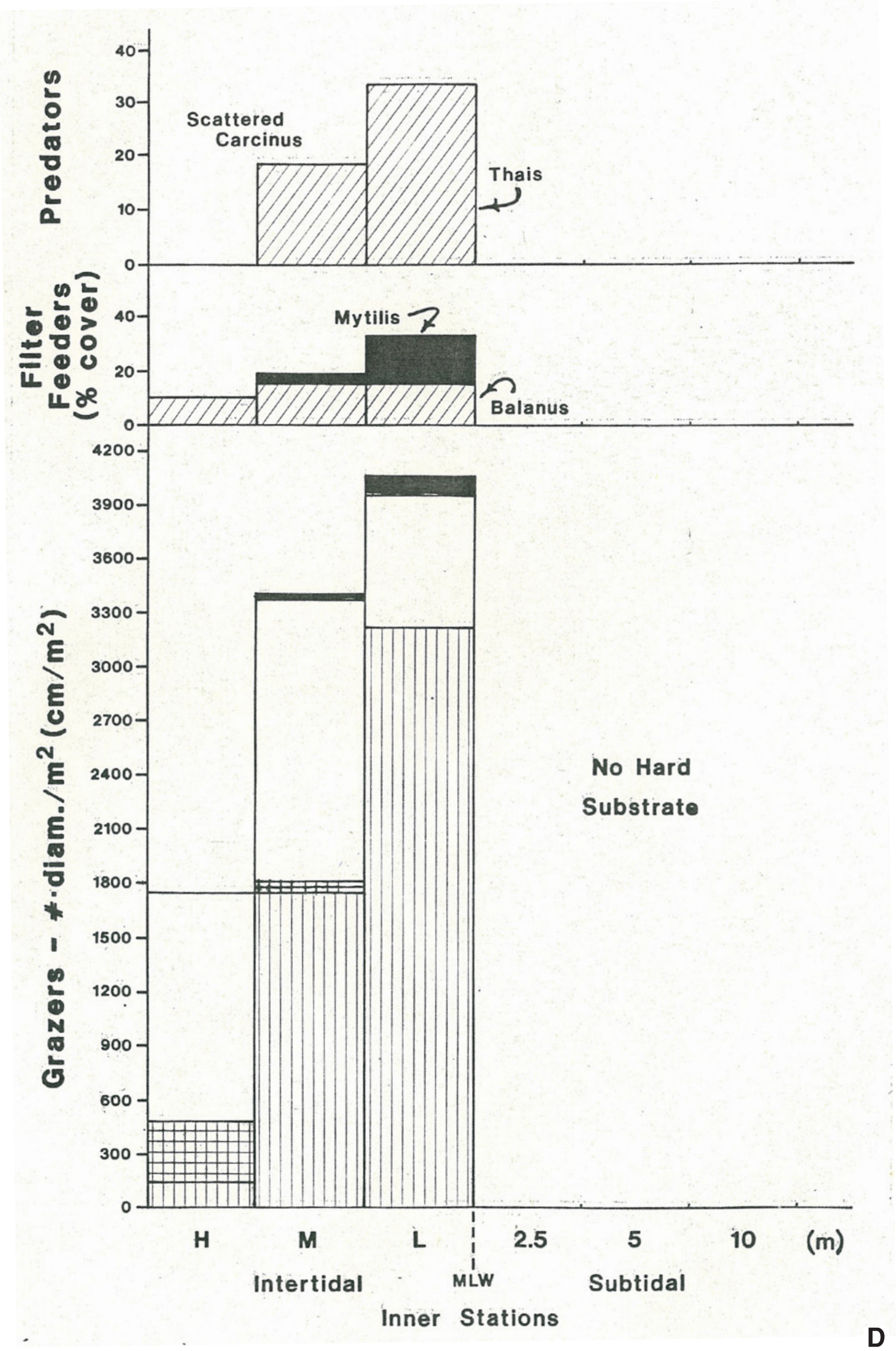


Figure 63A-D. Invertebrate populations, rocky intertidal and subtidal of Gouldsboro Bay.

Our discussion has centered around dominant plant *Ascophyllum nodosum*. The rockweed *Fucus vesiculosus* and a variety of filamentous and leafy green, brown and red algae, as well as a scattering of several red crusts, also occur in the intertidal, particularly in the more exposed areas. It seems likely that *Ascophyllum* possesses a decided growth advantage over these other species, but is slow to recover and re-colonize from a damaged or denuded state.

Based on productivity data of the various algal groups, from the literature (Doty, 1971), we have calculated a potential productivity for each algal group for each station and depth zone. The results, based on the standing crop for each group (Figure 64), suggests that at all intertidal stations and depth zones, except the outer region, *Ascophyllum* provides over 95% of the total primary productivity. At the outer station, leafy and fleshy, small macrophytes dominate the lower intertidal. As a result, the proportion of the total productivity of outer stations attributable to *Ascophyllum* is just under 70%.

At this writing, it would appear that most of the intertidal productivity of Gouldsboro Bay is centered in the alga *Ascophyllum*, and our preliminary discussion of energy flow in the bay system is based on this information and our extensive understanding of this species. Whether the productivity of filamentous algae matches the magnitude of primary production in

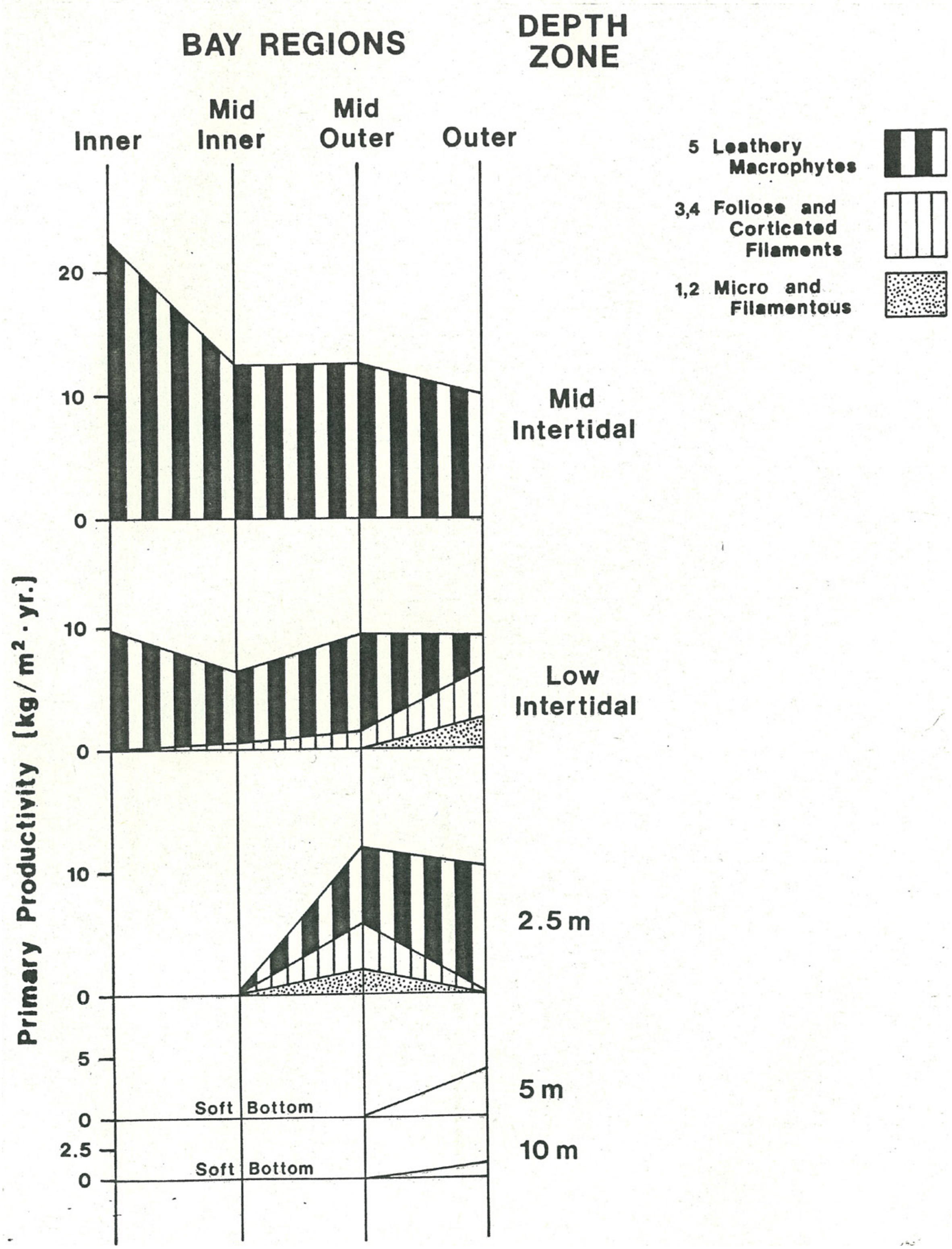


Figure 64. Estimated productivity of filamentous and foliose algae of the rocky inter-and subtidal.

Ascophyllum or not, the trophic pathway of small algae/littorinids/dog whelks/birds in the intertidal is an interesting one.

Mud Flats

The community structure of the macro benthos of soft bottoms, including intertidal flats is discussed below. Here our emphasis is on primary productivity. The muddy intertidal (Figure 65) occupies most of the upper reaches of the bay and next to open water and subtidal soft bottoms is the largest bay community at about 15% of total bay area. Nevertheless, in spite of the large area, because of the nature of the substrate and the severe winter conditions, primary productivity is quite low on flats. The percentage of organic material in the upper layers of the flats is quite high. Our analyses are underway at this time; however, preliminary results show that it is at least over 5% and probably closer to 10%. As discussed at several points in this paper, much of this organic material is undoubtedly detritus derived from macroalgal breakdown.

Algae (*Entermorpha* and diatoms) occur as primary producers on these flats. However, algal productivity is greatly outweighed throughout the summer by that of *Zostera marina* (eel grass) (Figures 65, 66). *Zostera* colonizes the mid-zone of the mud flats during the spring and grows through the summer. By late summer and early autumn, the flats have a dark green color from the air, and the *Zostera* at low tide provides an almost

Figure 65. Mud flat in late summer showing an extensive coverage of yearling Zostera (dark green).

Figure 66. Close up on flat showing a nearly complete cover of Zostera.

continuous cover over the mid-tide range of the flat. During January, shore fast ice along the flats gradually builds seaward, eventually covering most of Joy and West Bays during cold winter (Figures 34, 37). On very cold nights, at low tide, the *Zostera* is frozen into the ice sheet. With tide rise, the plants are pulled from the mud. By early spring, as the ice melts off, no trace can be found of *Zostera* on the flats. Thus, these mud flat communities, considering their large area, are a significant component of the productivity of the bay. However, growth of standing crop is renewed each spring; the plants are only yearlings and they enter the detritus food chain as drift along the shore, providing only about 5% of total Bay primary productivity (see below, Primary Productivity). As a result, mud flats are predominantly consumer communities mostly living on the primary productivity of the water column and the rocky intertidal.

Large mussel bars (Figures 67, 68) occur in Joy Bay and to a lesser extent West Bay. Although these features form the smallest biological community recognized in this study, they are particularly interesting both because they are the only organisms that significantly change the substrate aspect of their environment (like tropical reefs) and because of their potential economic value.

Marshes

Aerially, marshes are a relatively small component of

Figure 67. Mussel bars in Joy Bay at about a mean low water tide.

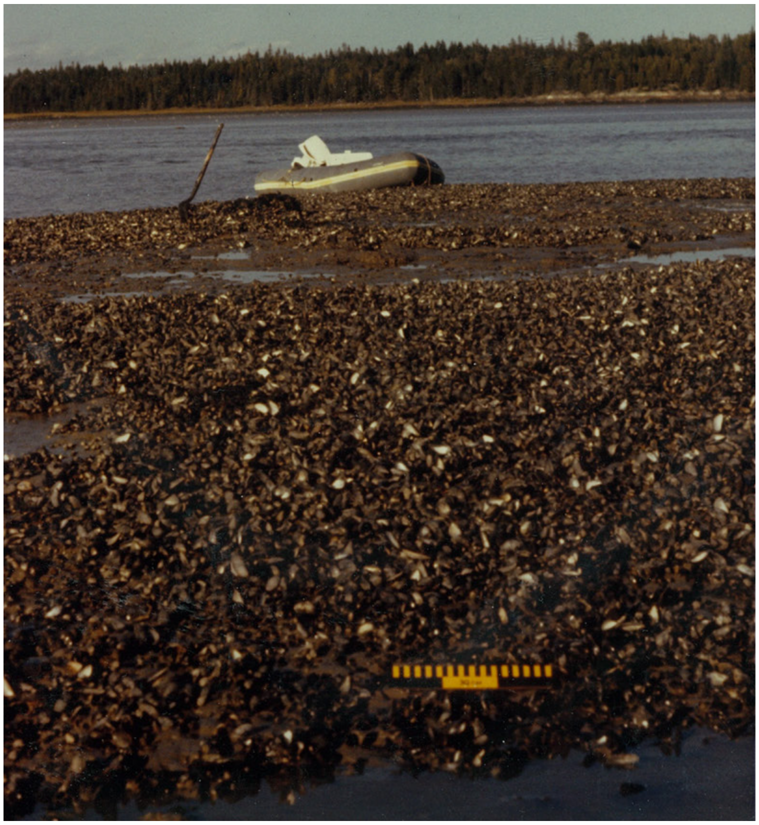


Figure 68. Close up of mussel bar on a Joy Bay mud flat.

Gouldsboro Bay, as they also are for most the Maine coast. The largest marsh in Gouldsboro Bay is Grand Marsh, at the southern end of the West Bay (Figures 30, 31). Fringing marshes, a few meters wide, are abundant around the upper reaches of West and Joy Bays (Figures 49), and Little Marsh is developed at the northeastern corner of West Bay (Figure 69). However, these structures are very small in area as compared to Grand Marsh. Although we carried out extensive geological studies on Grand Marsh, productivity studies were not performed. A significant literature exists on the productivity of east coast marshes, and this information is used to develop the ecosystem model discussed below.

Figure 69. Little Marsh in northeast West Bay.

Subtidal

Hard Bottoms

Next to the rocky, algal-covered intertidal, the most productive communities of colder shores of both the northern and southern hemisphere are "reefs" or “forests” of very large algae, typically kelps. Although very limited in areal coverage, the kelp community is known for its high productivity and its high diversity of organisms (Figures 70, 71, 72).

Typically in the eastern Gulf of Maine, the subtidal kelp community is limited by a lack of abundant hard substrate in the protected parts of bays. However, even where substrate is not a factor, kelp only extends from low water springs to various depths ranging from a very few meters to 15-20m. Where soft bottom is not a factor, the lower limit appears to be generally controlled by urchin grazing, which in turn is principally limited in shallow water by wave action. In the mid to inner parts of large bays, such as Frenchmans, Blue Hill and Penobscot, where substrate is not limiting and open ocean swell is virtually absent, urchin grazing limits the kelp community to very shallow depths and often removes it entirely. When the kelp is absent, a rocky bottom, at depths of 15-30m, depending on turbidity or often distance offshore, is occupied by a coralline-urchin community which typically contains abundant mussels (*Modiolus modiolus*), starfish (*Asterias forbesi*) and sea cucumbers (*Cucumaria frondosa*). Corallines are very low level primary

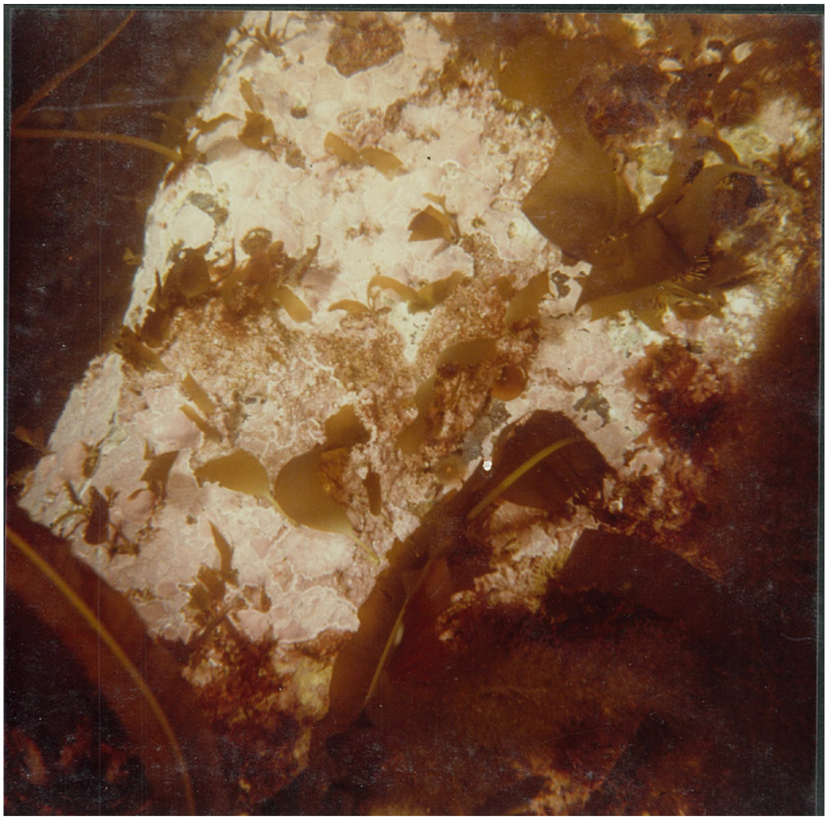


Figure 70. Shallow water (lm below mlw) with young Laminaria Kelps and the mid-ribbed Alaria kelp. The pink crustose coralline which underlies most kelp cover becomes the dominant algal form under heavy urchin grazing.

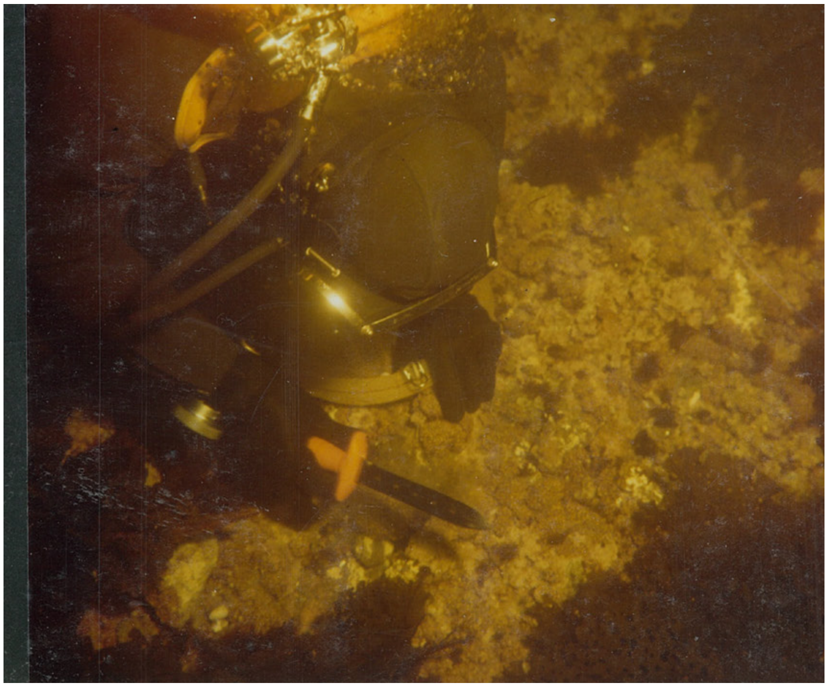


Figure 71. Lower end of the kelp zone at boundary of “armoured” bottom. The dominant kelp here is the perforated Agarum which is very low on the sea urchin food preference list.

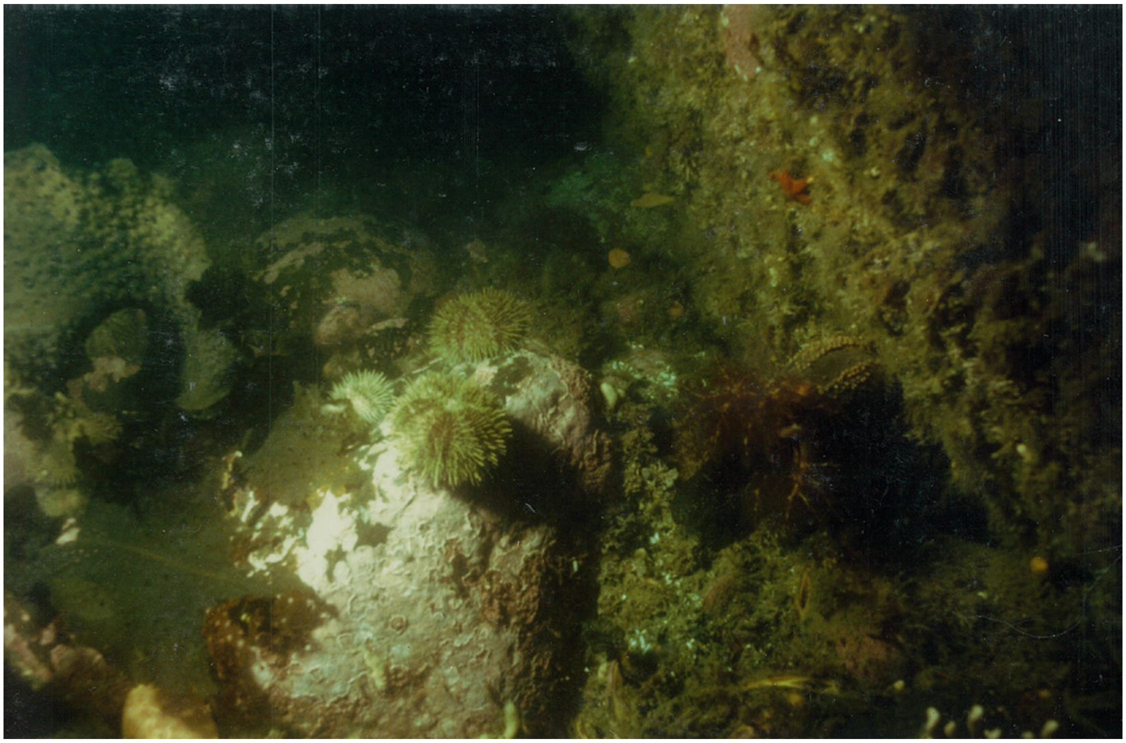


Figure 72. The urchin Strongylocentrotus droebachiensis, sea cucumber Cucumaria frondosa and mussel Modiolus modiolus

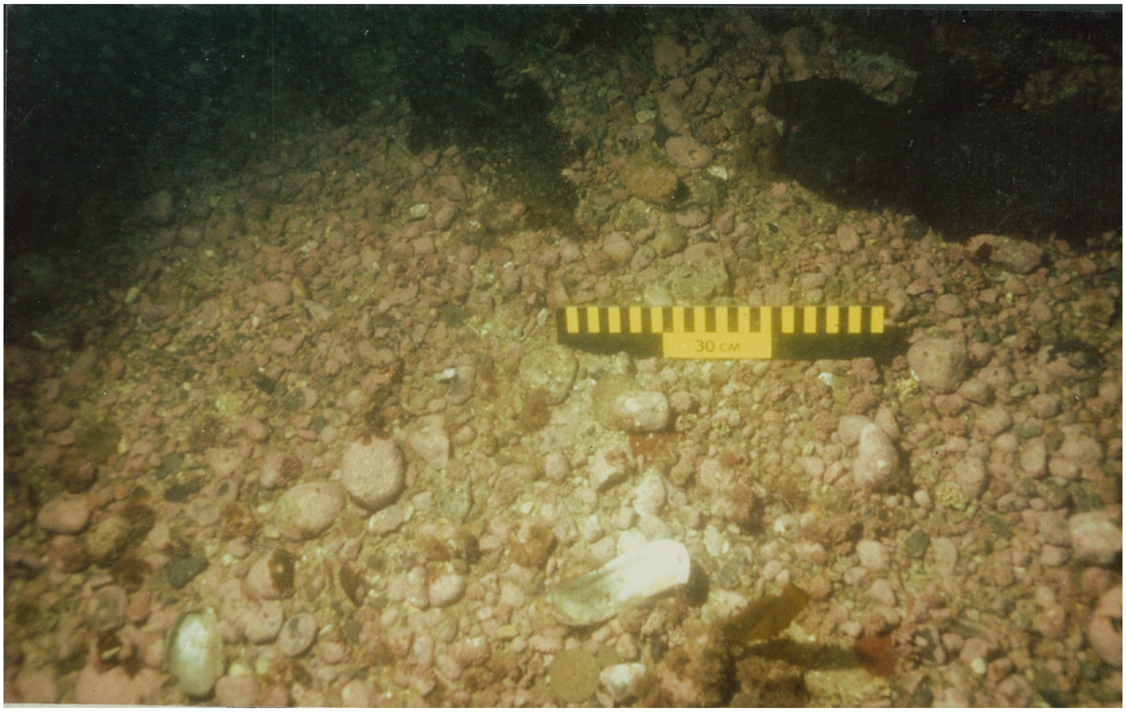


Figure 73. Armoured bottom inside the channel between Eastern Island and Bald Rock. The pebbles, which are constantly overturned become coated with coralline algae, principally Lithothamnium glaciale and Leptophytum laeve at this depth (60 feet).

producers as compared to kelps, and thus a community analogous to thorn-scrub has developed in these cases. Urchin abundance is probably limited to some degree by crab and lobster abundance. It is likely that heavy fishing of these crustaceans has some indirect influence on the productivity of subtidal rocky shores.

There is considerable depth zonation among the larger algae in the kelp community (Figures 70, 71, 72). *Alaria esculenta*, a mid-ribbed species, is the dominant plant in the upper meter on wave beaten shores; it is often absent in bays. *Laminaria saccharina* and *Laminaria longicruris* are the characteristic kelps of the mid-zone. At the lower end of the zone, the mid-ribbed and perforated *Agarum cribosum*, tends to dominate. The latter is quite resistant to urchin grazing and probably contains noxious compounds.

Subtidal algal biomass, productivity and herbivore population structure throughout the rocky areas of Gouldsboro Bay were studied in this project. The subtidal zone showed a number of demographic trends opposite to those found on the adjacent intertidal zone. Although scattered subtidal rocks and patches of kelp occur in the upper bay and into the mouth of both Joy and West Bays, as a continuous subtidal community, the kelp (or its replacement coralline) community is largely limited to the mid-outer and outer regions (Figure 53). Both inland along the bay shores and with depth, on the outer shores, the total plant biomass (Table 3) and kelp productivity decrease (Figure 64).

This is to be expected as a result of light limitations due to increasing depth and increasing turbidity.

At the outer stations, there is a marked increase in abundance of the green sea urchins with depth. Very few animals occur at 2.5m and the number and size of the animals greatly increase at 5m. A reduction in abundance then occurs at 10m probably due to the reduction of forage (Figure 63a,64). At the mid-outer stations, only a few animals were found in the subtidal zone. Thus, it would seem that, unlike in the larger bays and in more exposed locales, turbidity and substrate are far more critical in limiting the kelp community than *Strongylocentrotus droebachiensis*.

It has been shown that seasonal fluctuations in the growth rates of *Laminaria longicruris* vary with both location and exposure to wave action. Studies at Fox Point, Nova Scotia showed growth rates highest during January to June in sheltered areas as opposed to during March-June at more exposed areas (Mann, 1972). Chapman and Craigie (1977) studying the same exposed location at a later time found the highest growth rates to occur during roughly the same time. In Shag Bay, Nova Scotia, Gerard and Mann (1979) found growth rates highest during the period from May - September in the more sheltered area and during May - July in the more exposed site. These seasonal variations in production have been considered to be due to nutrient fluxes (Chapman and Craigie, 1977; Harlin and Craigie, 1978; Gagne et al, 1982). Boden (1979) found a maximum rate of elongation at a depth of 9m off Appledore Island, Maine. He suggested that reduced nutrients and higher temperatures at the surface were the growth-limiting factors.

Light penetration and irradiance are factors which vary greatly between seasons. Dieckman (1980) found that growth of *Laminaria pallida* was positively correlated with day length. John (1970) found a decrease in growth with increasing depth due to the gradual attenuation of light and Anderson et al (1981), working at Bic Island, St. Lawrence estuary, Canada found growth of *L. longicruris* to be regulated by irradiance and temperature. Exposure to wave action is another important factor which not only effects morphology (Chapman, 1973) but also productivity (Gerard and Mann, 1979). Gerard and Mann concluded that plants exposed to intense turbulence tended to have a lower productivity and that this condition can be understood in terms of growth. Thus, studies to date have concluded that nutrients, irradiance (depth and season), wave action and temperature can all regulate primary production in the subtidal kelp community. While emphasis has been placed on the role of nutrients, a consensus of opinions regarding the factor(s) most important in controlling primary production of the upper, subtidal, cold water community has not been reached.

It has long been recognized that sea urchins (*Stronglyocentrotus droebrachiensis* in the North Atlantic) are the primary grazers of kelp and therefore provide one of the major first steps up in the shore food weds (Duggins, 1981; Lang and Mann, 1976). Several studies have been directed towards determining rates of consumption by these effective grazers. However, none of these investigations has been tied to in-situ consumption, in a variety of shore environments, where actual kelp production and standing crop were also known.

The distribution of the primary benthic communities in Gouldsboro Bay and off-lying waters is shown in figure 74. The stations shown in figure 75 were selected after surveying the biomass of invertebrates and macrophytic algae over large areas of hard bottom in Gouldsboro Bay and along the shores of the exposed region. Stations were chosen as being visually representative of the regions discussed. For more detailed studies formal transects were established with anchors, polypropylene line and buoys. Samples and measurements of biomass and growth were taken at depths of 2.5m, 5.0m and 10.0m.

Biomass measurements at each station and depth were accomplished by randomly throwing 16 quadrats, 1/16m^2, and collecting all macroalgal material under the quadrat. While all collected kelp was tabulated, only *Laminaria longicruris, Laminaria digitata* and *Agarum cribrosum* were used for quantitative analysis. Samples of *Alaria esculenta, Polysiphonia* spp., *Desmarestia* spp. and a variety of red species (*Chondrus crispus, Euthora cristata* and *Phycodrys rubens*) were tabulated

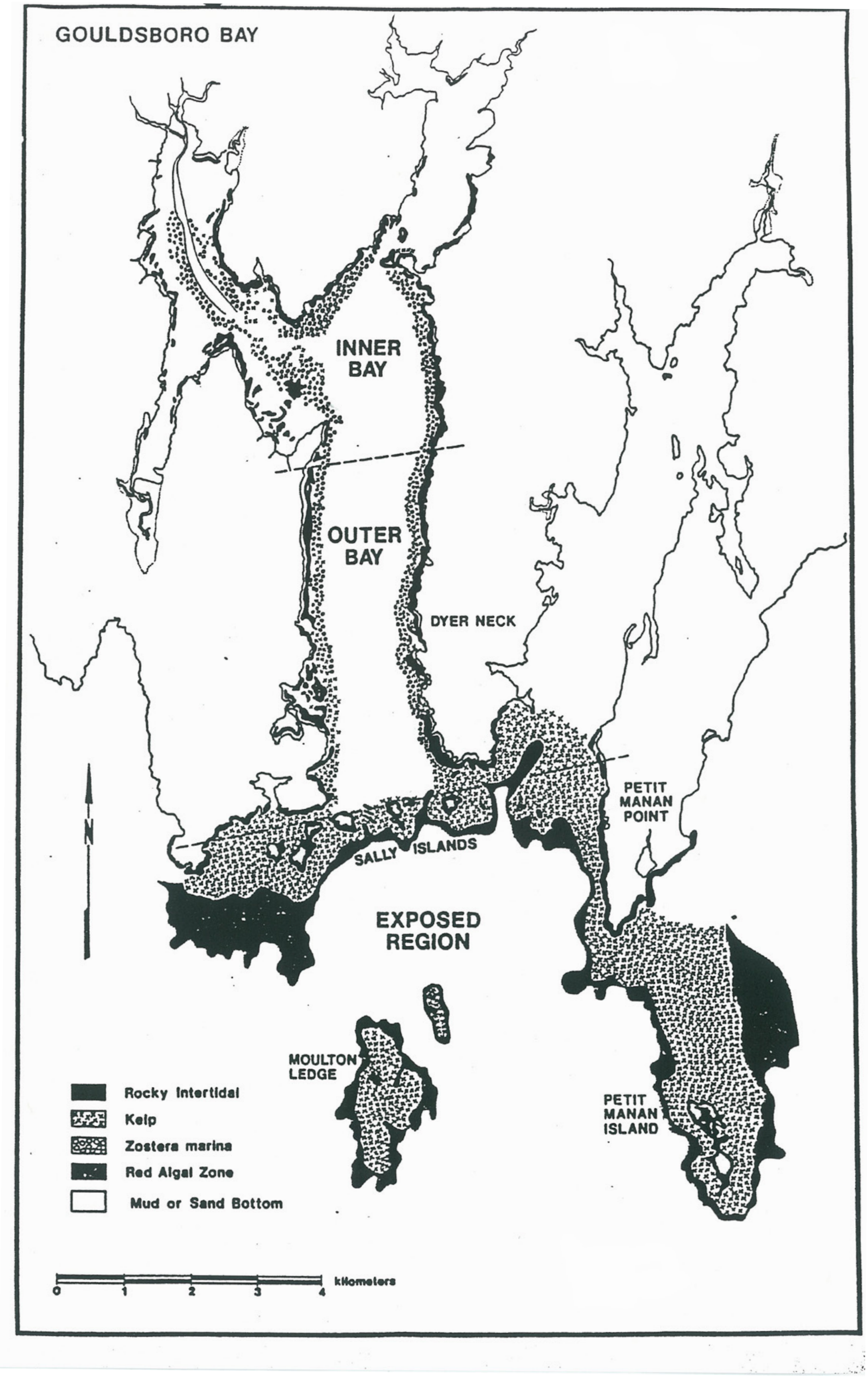


Figure 74. Principal macroalgal and Zostera communities in Gouldsboro Bay and its offlying waters.

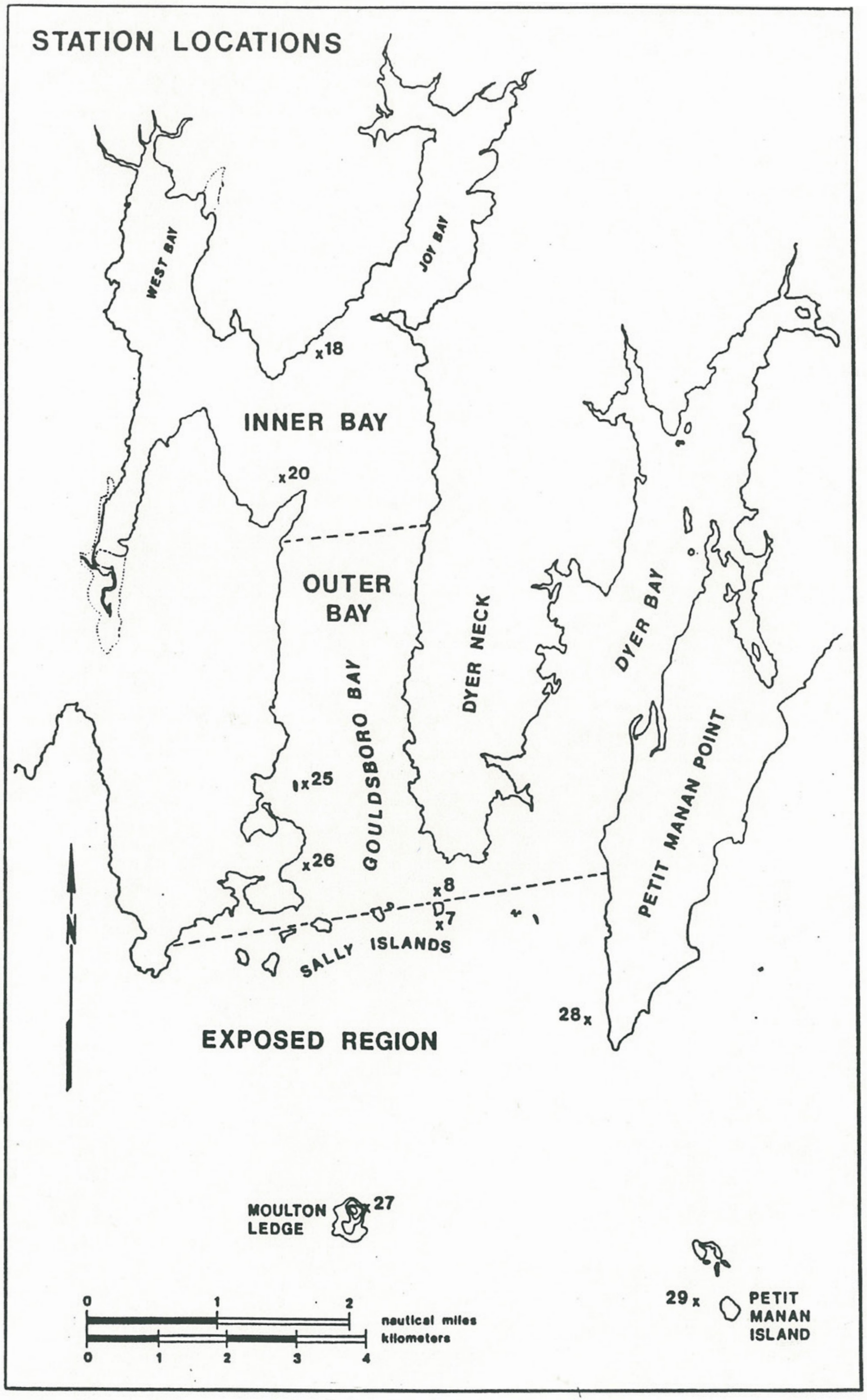


Figure 75. Station locations for studies of benthic, subtidal macroalgae.

but only recorded for biomass counts. Samples were returned to an on-site ship laboratory for identification and weighing. Elongation measurements were made by tagging 23-26 individual plants at each station and depth with orange surveyor's ribbon, and punching a hole in the frond 20cm above the junction of blade and stipe (Boden, 1979). Subsequently the separation of the hole that occurs with meristematic growth was measured. Where plants remained intact, as most plants did, the whole tagged plant was collected. The growth section was excised and the biomass increase determined by weighing (wet) to yield production in g (wet)/m^2/day. To determine dry weights, a regression of wet to dry weights was run (.97).

Light data were collected with a submersible Li-Cor Li-185A light meter at depths of 2.5m, 5.0m and 10.0m. Readings were taken only on sunny days between 1200 and 1300 hours. They are therefore seasonal maxima for the environments studied. Nutrients were analyzed using a standard Hack Test kit and auto-analyzer. To estimate live biomass and abundance of the sea urchin *Strongylocentrotus droebachiensis*, 1/16m^2 quadrats were thrown at each station and depth. Urchin diameters were measured and recorded. A regression of wet weight against diameter was established for 16 animals, and from that standard, biomass figures for each depth/station were tabulated. Urchin consumption rates were estimated using three 0.25m^2 cages made of "Vexar" plastic that were weighted and sunken to a depth of 5.0m.

A weighted quantity of *L. longicruris* was placed in all three cages. Three weighed urchins were placed inside two of the cages. The third cage was used as a control. After 2-3 days the kelp was removed and re-weighed. The difference in kelp weight approximated the amount of kelp consumed. No account for leaching or growth was considered. The experiment was run five consecutive times and in each case exhibited approximately the same results. These results were analyzed by regression analysis using urchin weight against kelp consumption. The weight of other urchins at different depths and stations were utilized in this regression. Unless otherwise indicated, statistical confidence levels are 95%.

The three species treated here *Laminaria longicruris, Laminaria digitata* and Agarum cribrosum form 88.3% ± 7.1 (S.D.) of the subtidal algal biomass at the stations sampled. Biomass data for the dominant species of kelp are shown in figure 76 for each region and depth. *L. longicruris* dominates all regions and depths during the summer and fall, except at the 10.0m exposed region, which is dominated by *A. cribrosum*. In the summer, in shallow water at more protected stations, or at moderate depths in exposed areas, *L. longicruris* makes up 65% or more of the total kelp biomass. In the shallow exposed areas *L. digitata* approaches *L. longicruris* in abundance in the summer. Massive reductions in standing crop of *L. longicruris* due to wave action occurs from late summer and especially in fall to late winter at all depths and regions. *L. digitata* does not follow this same trend in the outer bay region. It does so to lesser extent in the exposed region, so that by spring *L. digitata* equals or exceeds *L. longicruris* in abundance. While *A. cribrosum* is a considerably smaller element in the kelp community as a whole, at the lower end of the kelp zone, it can equal or exceed other *Laminaria* spp. in abundance. *A. cribrosum* which occurs only in small quantities in shallow water, and the other dominant kelp species at greater depth are little affected seasonally. The largest drop in biomass of *L. longicruris* occurs at 2.5m in the exposed region from late summer to winter (Figure 76). Large quantities of kelp are thrown up on the beaches every winter and spring as a result of physical dislodgement.

Frond elongation (as cm/d) and net primary production (as $g/m^2/d$) measurements are presented in figures 77 and 78. Biomass production is expressed as $g(wet)/m^2/d$ to eliminate problems of growth comparisons for plants with fronds of different widths.

Maximum elongation rates of 1.2 cm/d for *L. longicruris* occurred at a depth of 2.5m in the exposed region during late July - early August. The minimum, elongation of *L. longicruris* of 0.07cm/d occurred in the outer bay at 10.0cm depth. *L. longicruris* showed maximum elongation rates in summer for all depths at exposed stations. Marked drops in elongation occurred in the fall and winter. The outer and inner bay regions showed an increase in elongation from summer/fall to later winter.

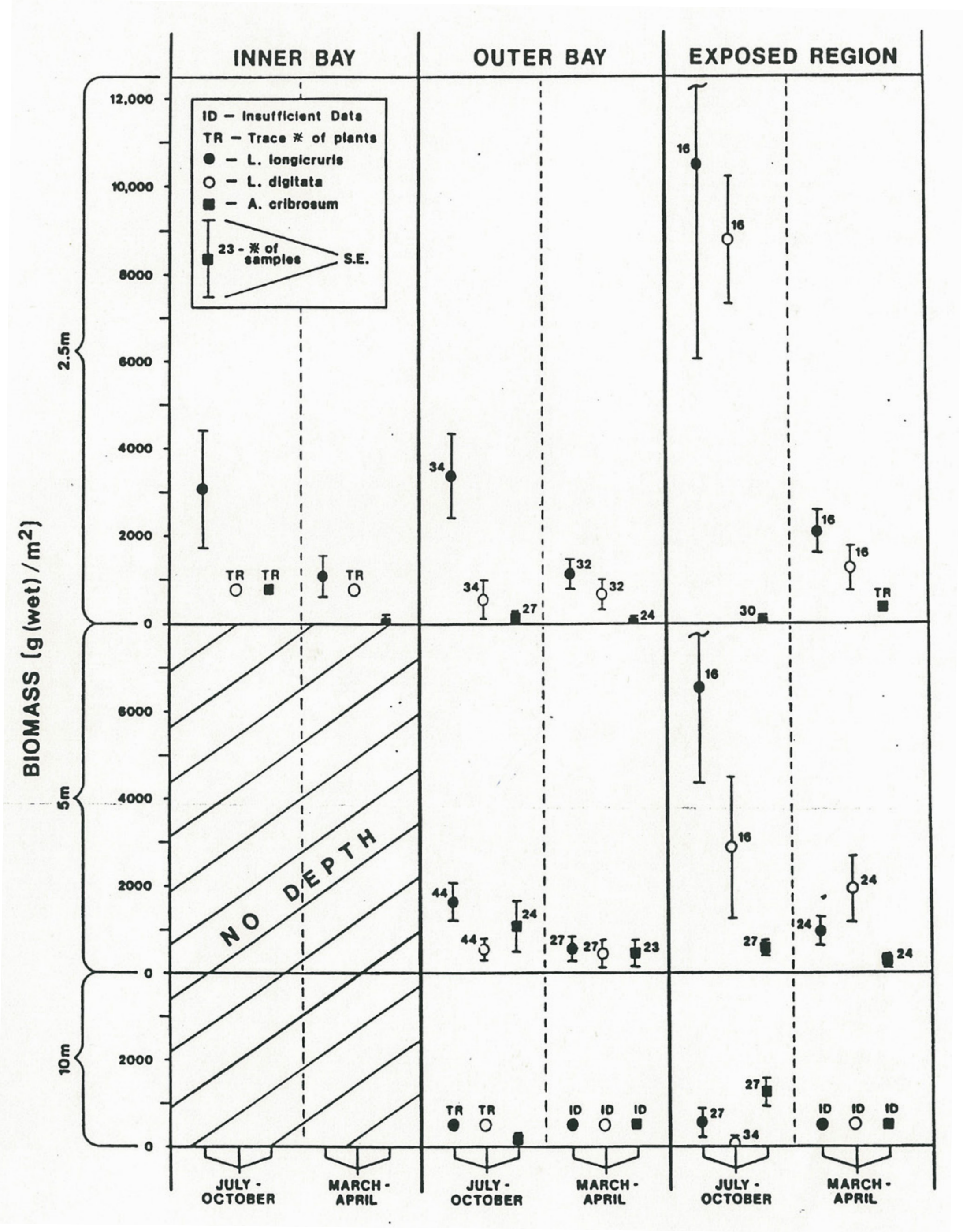
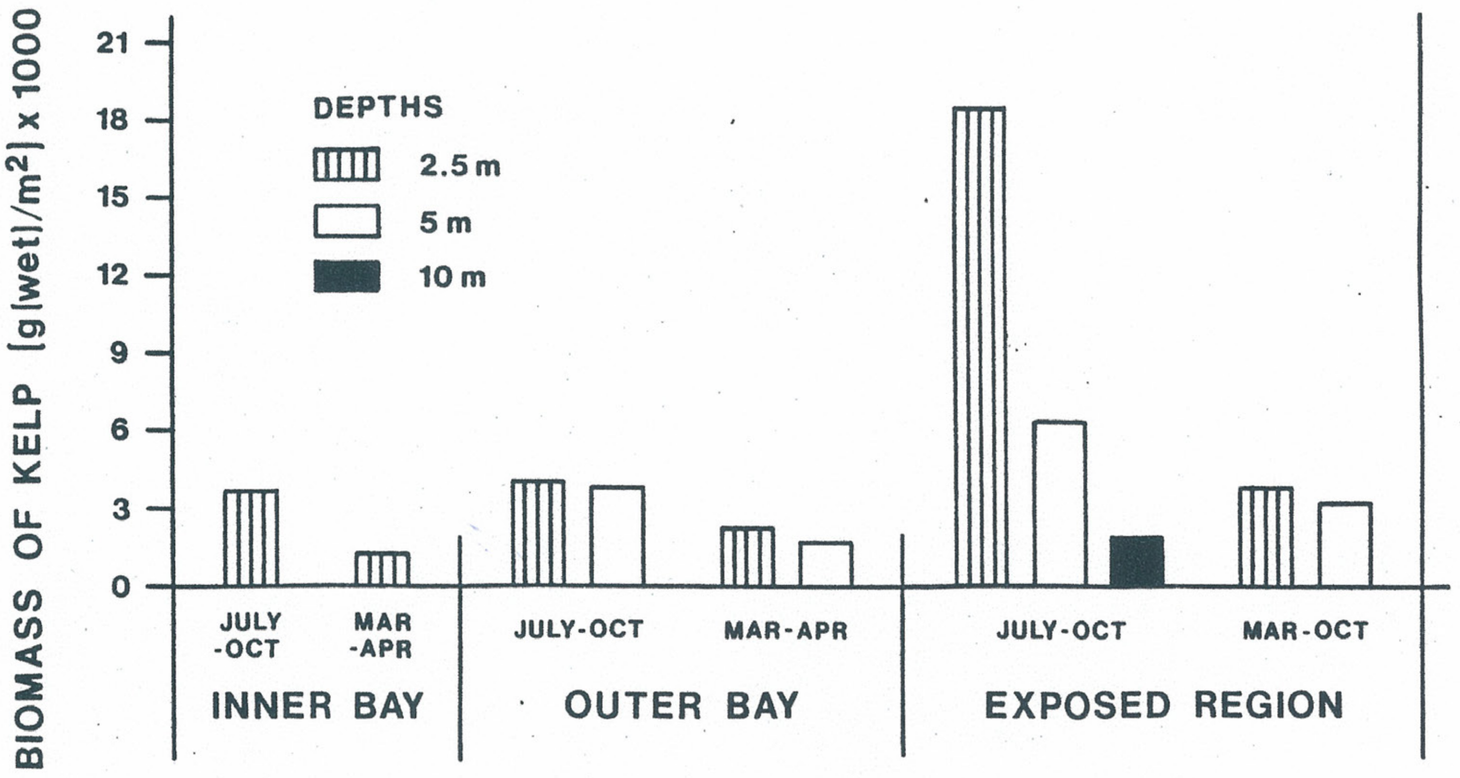


Figure 76, Biomass (standing crop) of dominant kelp species,by season, in the Gouldsboro Bay area. (a) comparison of mean biomass in the inner Bay and offshore.

Figure 76A, Biomass (standing crop) of dominant kelp species,by season, in the Gouldsboro Bay area. (a) comparison of mean biomass in the inner Bay and offshore.



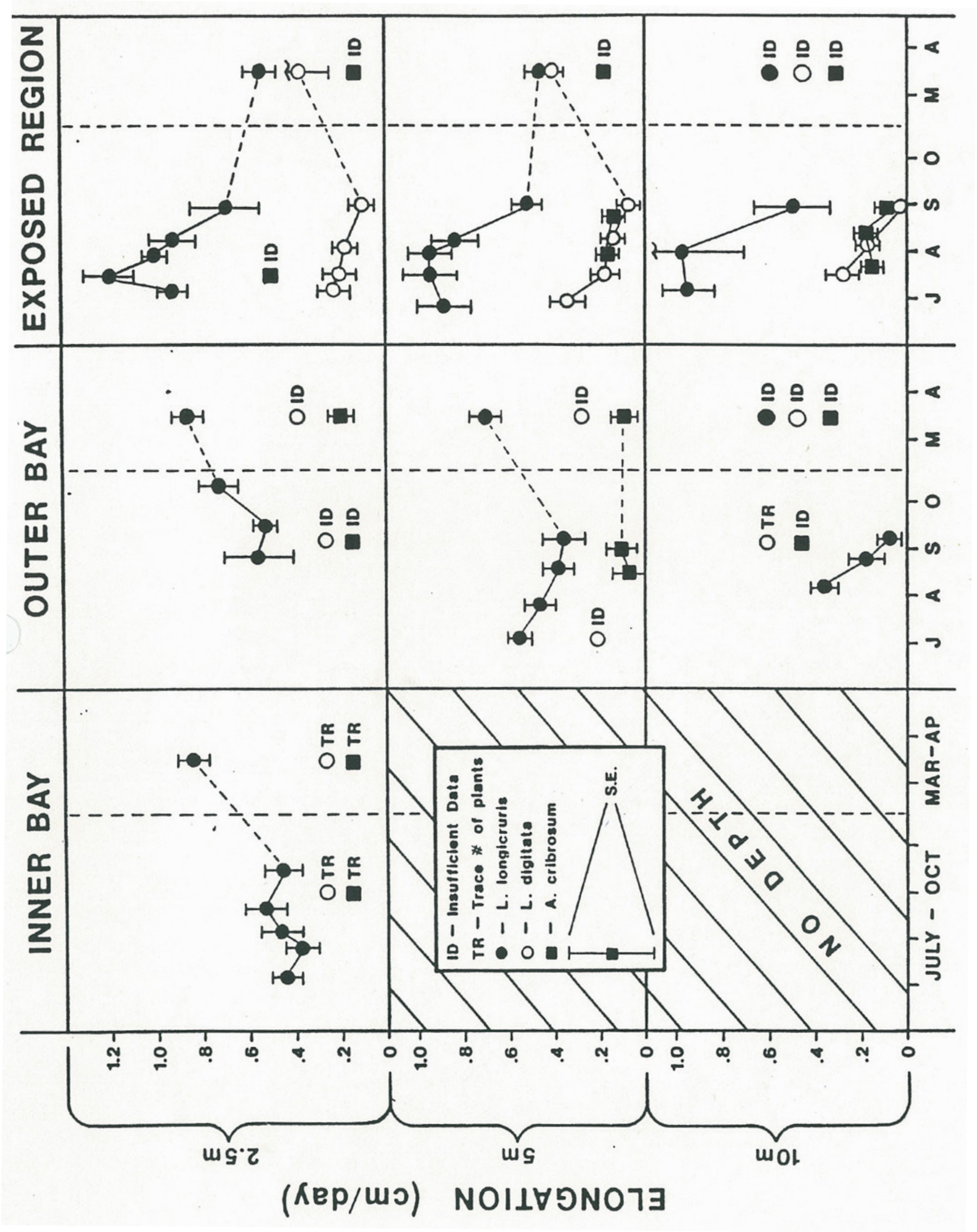


Figure 77. Rates of elongation of dominant kelp species, by season, in the Gouldsboro Bay area.

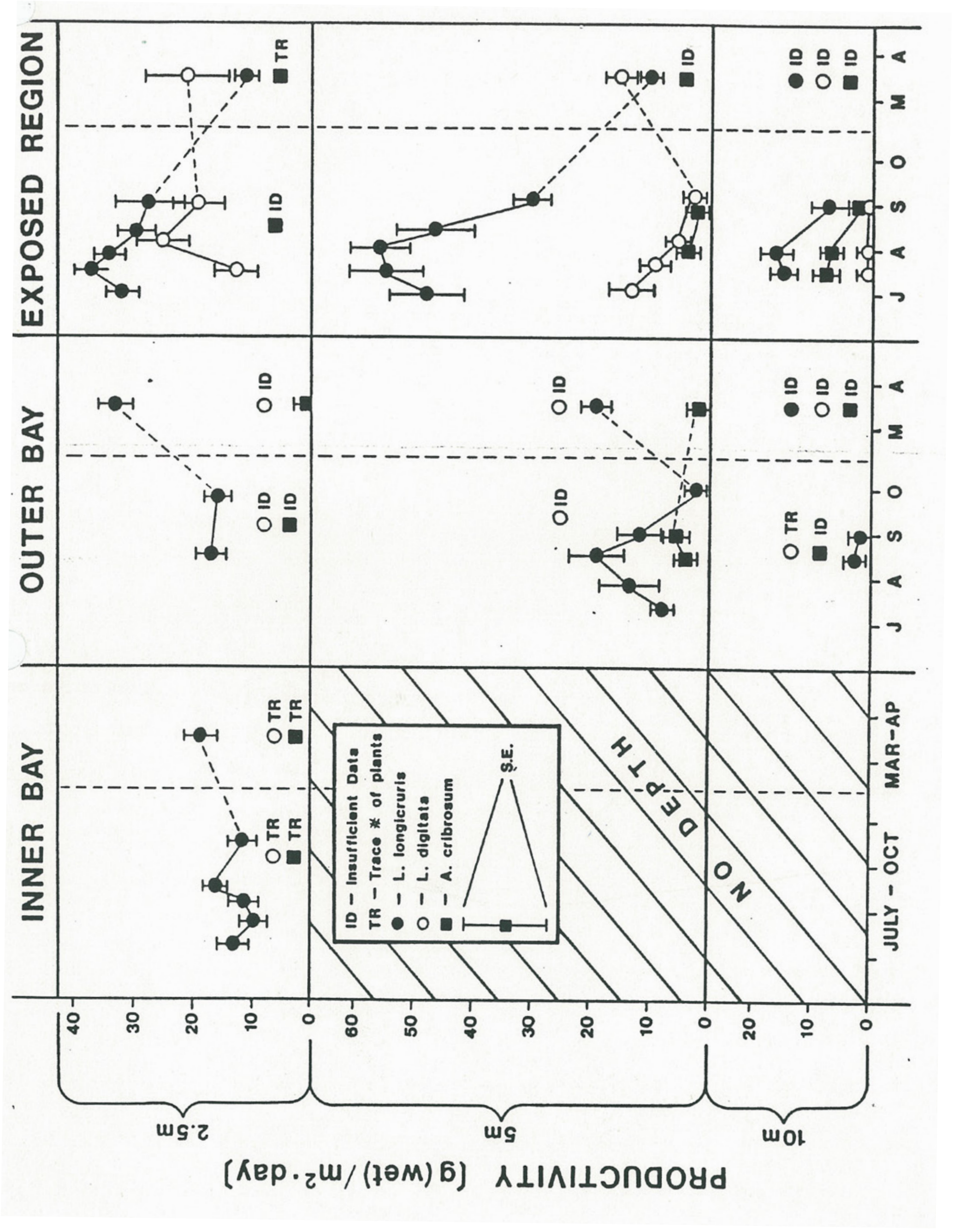


Figure 78. Primary production for dominant kelp species as a function of season and region in the Gouldsboro Bay area. These data were derived from information on number of plants per m2, elongation rates and mean frond widths. (a)Comparison of productivity in the inner and outer Bay and offshore.

Figure 77 shows an opposite trend for *L. digitata*, with a maximum elongation rate of 0.4cm/d at all depths during March - April in the exposed region. Rates were not measured for *L. digitata* in the inner bay area as an insufficient number of plants were present there to obtain reliable data, The elongation rates of *A. cribrosum* were generally significantly lower (by t-test) than those for *L. longicruris* throughout the year (Figure 77). However, in the exposed region, elongation rates of *A. cribrosum* equaled or exceeded that of *L. digitata*.

Production rates in g(dry)/m^2/d, and are derived from the number of plants/m^2, the elongation rate and the mean frond width (Figure 78). The highest rate of production in *L. longicruris* was 57.0g/m^2/d. This occurred at 5.0m in the exposed region during late July early August. A gradual increase in production is seen from the inner bay to the outer bay, and a more pronounced increase from the outer bay to the exposed region for *L. longicruris* during the summer and fall period at all depths studied. During late winter, production of *L. longicruris* drops from the outer bay to the exposed region at 2.5 and 5.0m.

Production of *L. digitata* is higher during the late winter than that of L. *longicruris* for the 2.5 and 5.0 exposed regions (Figure 78). While this trend is not apparent in the elongation data for the two species (Figure 77), the broader frond width, and the sometimes greater number of plants, provide for greater biomass production.

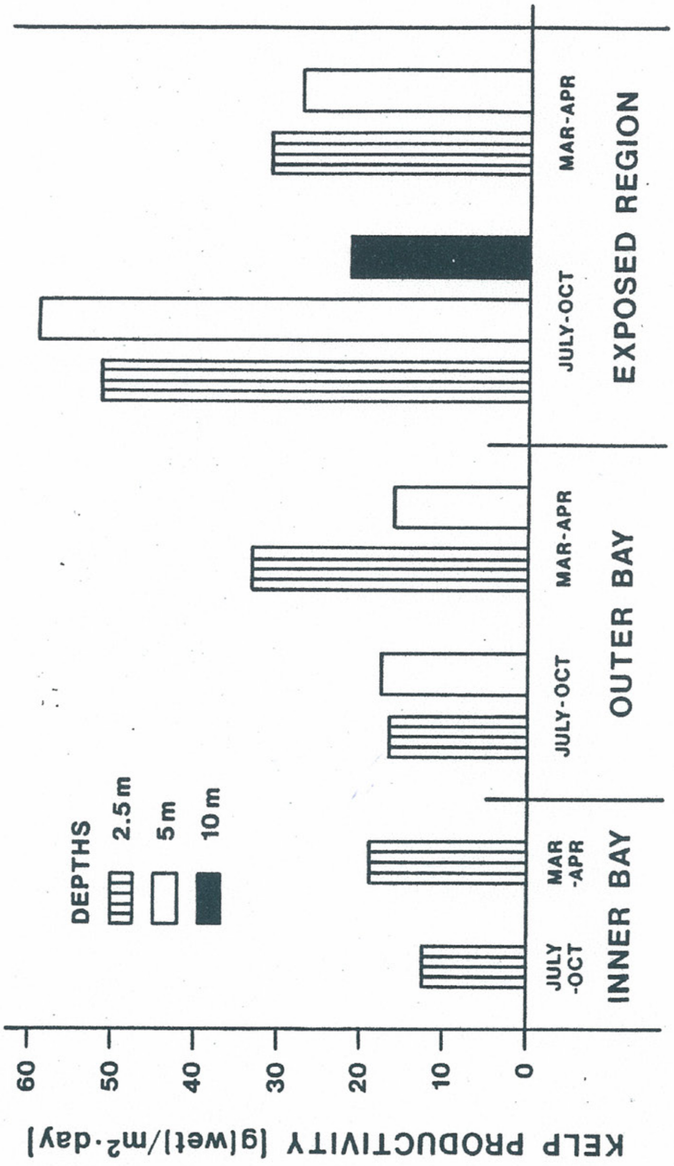


Figure 78A. Primary production for dominant kelp species as a function of season and region in the Gouldsboro Bay area. These data were derived from information on number of plants per m2, elongation rates and mean frond widths. (a)Comparison of productivity in the inner and outer Bay and offshore.

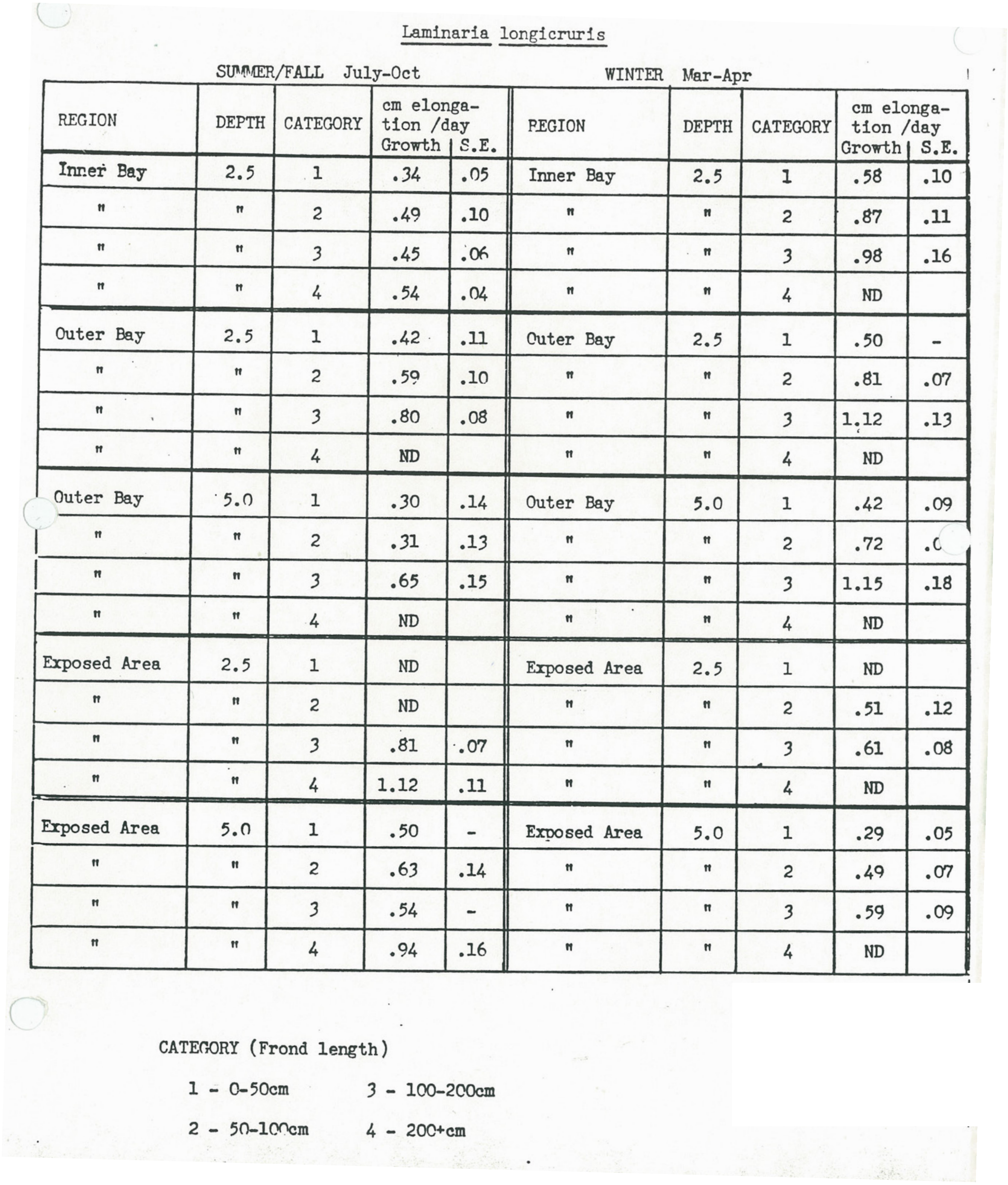
In *Laminaria longicruris*, frond width values were: inner bay, mean = 51.3cm ± 11.6; outer bay mean = 34.8cm ± 7.5; exposed mean = 20.6 ± 4.7; (N=16). Thus, the mean width of *L. longicruris* fronds decreased as wave action increased from the upper bay to the exposed region. Table 5 indicates that plants with larger fronds tend to elongate faster than smaller (younger) plants. During the summer and fall, plants in the inner and outer bay regions show growth rates that are lower than winter growth rates in that region. In general, the reverse trend is seen in the exposed region where growth rates tend to be lower in the winter.

Light energy at sampled depths for each season are given in Table 6. Light is reduced with depth and distance into the bay. In exposed areas, at 2.5m depth, light levels in the summer are about one-third of those reaching the water surface. This contrasts with a light energy level that is about one-sixth the level at the surface in the upper bay.

At all seasons and stations, nutrients are relatively high (Table 7), probably as a result of the intense tidal action that occurs on this part of the Maine coast. This considerable mixing effect likely prevents nutrient depletion of primary production. However, of particular interest in a productivity context is the apparent nutrient reduction into and up the bay, particularly in the later winter, early spring.

Data on sea urchin numbers and biomass indicate a

Table 5. Growth rates of Laminaria longicruris in Gouldsboro Bay and offlying waters.



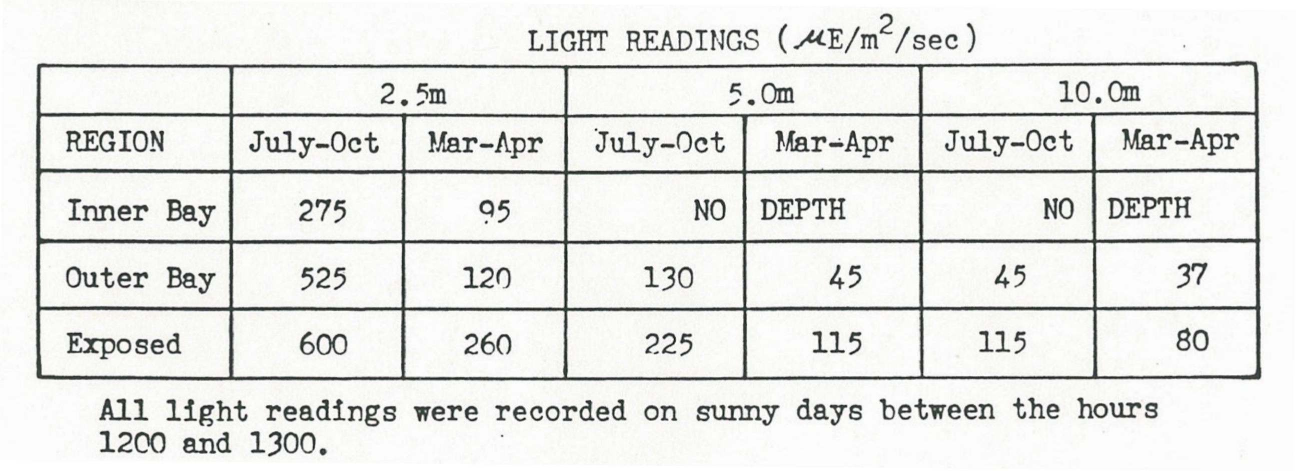
Laminaria longicruris

SUMMER/FALL July-Oct					WINTER Mar-Apr				
REGION	DEPTH	CATEGORY	cm elongation /day Growth	S.E.	REGION	DEPTH	CATEGORY	cm elongation /day Growth	S.E.
Inner Bay	2.5	1	.34	.05	Inner Bay	2.5	1	.58	.10
"	"	2	.49	.10	"	"	2	.87	.11
"	"	3	.45	.06	"	"	3	.98	.16
"	"	4	.54	.04	"	"	4	ND	
Outer Bay	2.5	1	.42	.11	Outer Bay	2.5	1	.50	-
"	"	2	.59	.10	"	"	2	.81	.07
"	"	3	.80	.08	"	"	3	1.12	.13
"	"	4	ND		"	"	4	ND	
Outer Bay	5.0	1	.30	.14	Outer Bay	5.0	1	.42	.09
"	"	2	.31	.13	"	"	2	.72	.0
"	"	3	.65	.15	"	"	3	1.15	.18
"	"	4	ND		"	"	4	ND	
Exposed Area	2.5	1	ND		Exposed Area	2.5	1	ND	
"	"	2	ND		"	"	2	.51	.12
"	"	3	.81	.07	"	"	3	.61	.08
"	"	4	1.12	.11	"	"	4	ND	
Exposed Area	5.0	1	.50	-	Exposed Area	5.0	1	.29	.05
"	"	2	.63	.14	"	"	2	.49	.07
"	"	3	.54	-	"	"	3	.59	.09
"	"	4	.94	.16	"	"	4	ND	

CATEGORY (Frond length)

1 - 0-50cm	3 - 100-200cm
2 - 50-100cm	4 - 200+cm

Table 6. Subtidal light levels (uE/m2/sec) in Gouldsboro Bay waters.

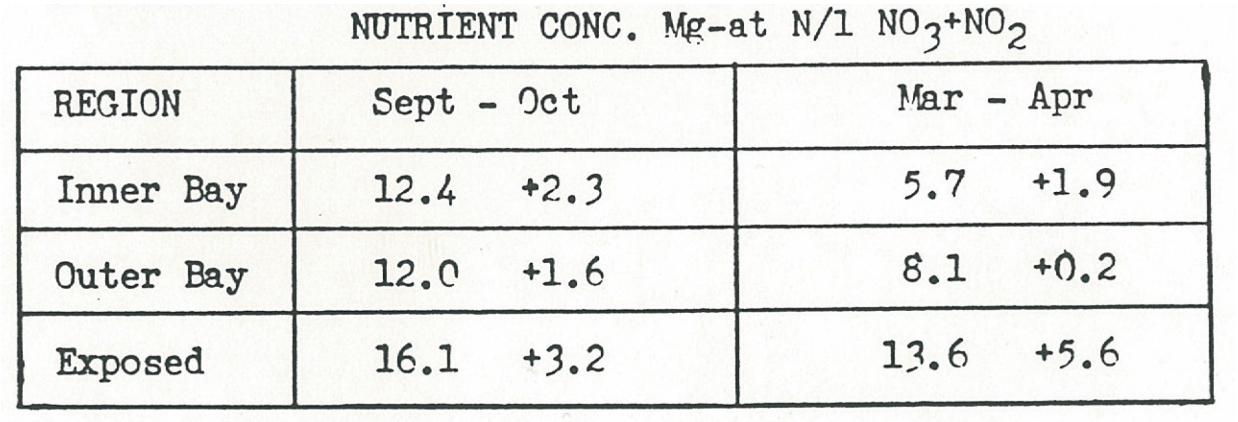


LIGHT READINGS ($\mu E/m^2/sec$)

	2.5m		5.0m		10.0m	
REGION	July-Oct	Mar-Apr	July-Oct	Mar-Apr	July-Oct	Mar-Apr
Inner Bay	275	95	NO	DEPTH	NO	DEPTH
Outer Bay	525	120	130	45	45	37
Exposed	600	260	225	115	115	80

All light readings were recorded on sunny days between the hours 1200 and 1300.

Table 7. Nutrient concentrations in Gouldsboro Bay waters.



NUTRIENT CONC. Mg-at N/1 NO_3+NO_2

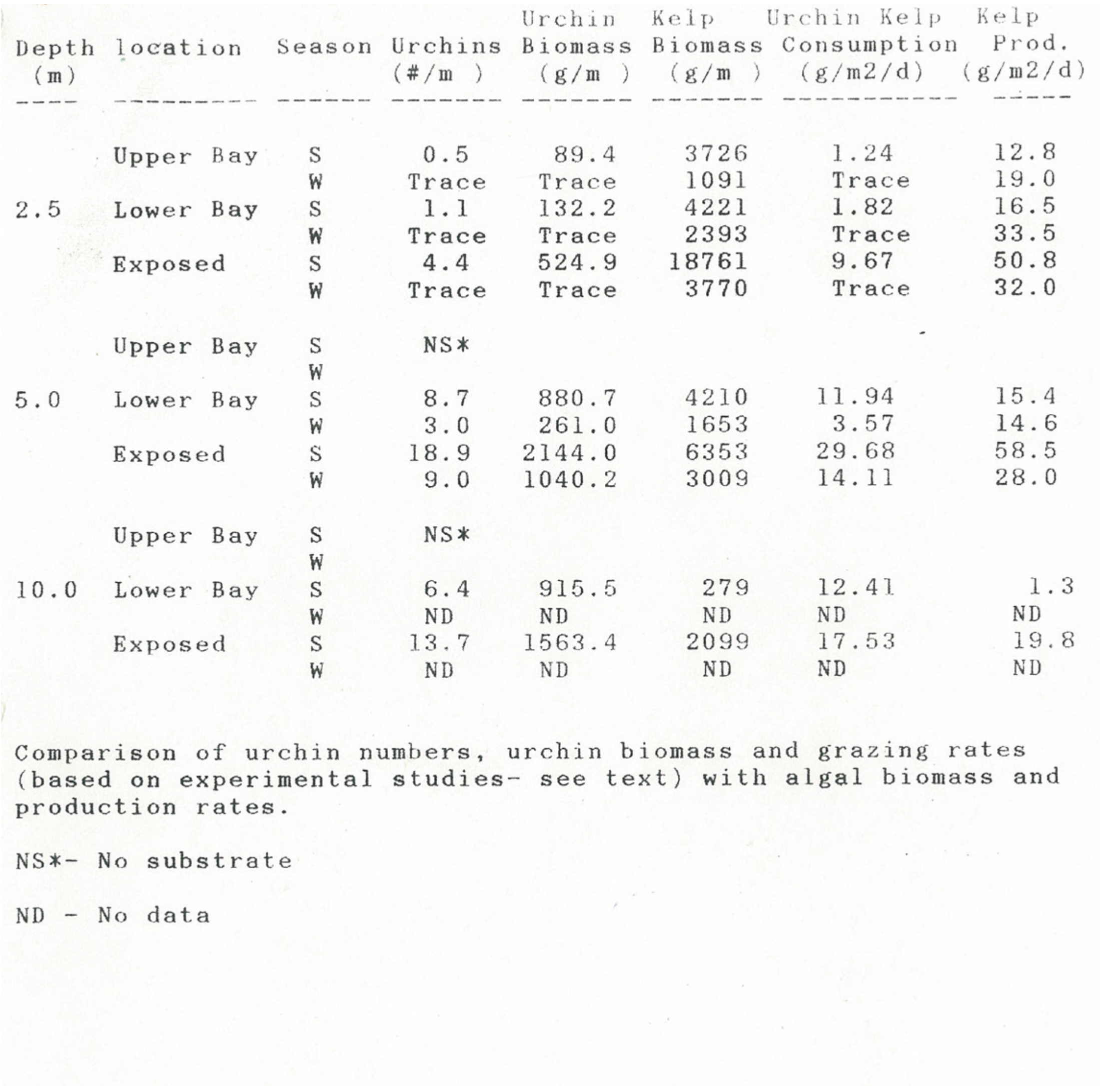
REGION	Sept - Oct	Mar - Apr
Inner Bay	12.4 +2.3	5.7 +1.9
Outer Bay	12.0 +1.6	8.1 +0.2
Exposed	16.1 +3.2	13.6 +5.6

conspicuous drop in the number of urchins/m^2 from the summer and fall to late winter (Table 8). The biomass of kelp consumed/m^2 also dropped at those depths having fewer urchins. Urchins were most abundant at the 5.0m depth at all sites, regardless of season. This region also had the most productive subtidal algal community (Figure 78).

The sum of the biomass values for the three predominant kelp species represents greater than 88% of the total algal biomass. These species are considered to provide a valid estimate of net primary productivity for the plant community as a whole. During the summer, mean plant biomass at the exposed stations at 2.5m depth is nearly 20,000g(wet)/m^2. Moving further into the bay, extending to greater depths, or winter sampling, are all accompanied by considerably reduced levels of biomass. In the exposed area, total kelp biomass at 5m is about 60% of that in shallower water. Otherwise, at no other location, depth or season did biomass reach more than 20% of the summer, exposed, 2.5m biomass values. These differences in biomass are statistically significant (by t-test), and visual observations at a wide variety of sites throughout the region sampled indicated that this pattern is typical of the area. These data also suggest that optimum conditions for growth and retention of biomass produced exist in the shallow exposed portions of the coast during the summer.

Figure 76 shows that the decrease in biomass for *L. digitata*

Table 8. Comparison of green sea urchin numbers, biomass andgrazing rates with algal biomass and production rates.



Depth (m)	location	Season	Urchins (#/m)	Urchin Biomass (g/m)	Kelp Biomass (g/m)	Urchin Kelp Consumption (g/m2/d)	Kelp Prod. (g/m2/d)
	Upper Bay	S	0.5	89.4	3726	1.24	12.8
		W	Trace	Trace	1091	Trace	19.0
2.5	Lower Bay	S	1.1	132.2	4221	1.82	16.5
		W	Trace	Trace	2393	Trace	33.5
	Exposed	S	4.4	524.9	18761	9.67	50.8
		W	Trace	Trace	3770	Trace	32.0
	Upper Bay	S	NS*				
		W					
5.0	Lower Bay	S	8.7	880.7	4210	11.94	15.4
		W	3.0	261.0	1653	3.57	14.6
	Exposed	S	18.9	2144.0	6353	29.68	58.5
		W	9.0	1040.2	3009	14.11	28.0
	Upper Bay	S	NS*				
		W					
10.0	Lower Bay	S	6.4	915.5	279	12.41	1.3
		W	ND	ND	ND	ND	ND
	Exposed	S	13.7	1563.4	2099	17.53	19.8
		W	ND	ND	ND	ND	ND

Comparison of urchin numbers, urchin biomass and grazing rates (based on experimental studies- see text) with algal biomass and production rates.

NS*- No substrate

ND - No data

as compared with that for *L. longicruris*, is not as drastic in the outer bay and 5.0m exposed regions from summer to fall and late winter. This suggests that the morphological differences (Chapman, 1974) between the two species provides *L. digitata* with greater relative resistance to wave action than *L. longicruris*. However, the massive drop in biomass in the shallowest exposed zone also shows that *L. digitata* is susceptible to dislodgement in intense turbulence.

A plot of total kelp production (g(wet)/m^2/d in figure 78A) shows a pattern similar to that of biomass, indicating that standing crop, in part, results directly from the quantity produced during a given period. Outer bays and exposed regions on the Maine coast are probably characterized by year round production rates in the 15-50g (wet)/m^2/d range. Much if this production is cast up on the beach each winter, but by the end of the summer, standing crops of 5kg g/m^2 to 10kg g/m^2 (with levels to 20kg g/m^2 in favorable areas) occur on most outer shores. The trend of reduction in production during the summer months from the exposed areas to the inner bays areas is also marked and generally parallels that of biomass. However, further examination of the relationship between biomass and productivity reveals some very striking differences in pattern. Winter productivity within the bay at 2.5m depth exceeds summer production by 45% to over 100%, whereas the exposed region at 2.5m shows a 40% reduction in winter.

Contrary to what was expected, there was no significant relationship between nitrogen levels and productivity. Nitrogen (NO_2 and NO_2) levels were above 10 microM (the saturation level for growth, Chapman et al, 1978) during late summer. This probably rules out nitrogen as the primary growth-limiting factor during this season. Elongation/day is lowest in the exposed region at both 2.5 and 5.0m in late winter when nitrogen levels are highest also indicating that nitrogen is not a primary growth control factor. Also, the inner bay regions show winter productivity rates significantly higher than those measured in the summer. In summer, productivity drops sharply from exposed areas to in-bay areas far out of proportion to corresponding light limitation.

A model of primary control of productivity by wave action followed by light limitation would explain the entire pattern of kelp productivity found in this investigation. While sea and swell data for the coast are available, they apply to offshore areas and are difficult to interpret. Considerable small boat field observation indicated that wave energy, sea and swell, generally decrease from the exposed region into the inner bay regions. The productivity data presented here strongly suggests a direct relationship between wave energy and kelp growth in all regions studied during both the summer and winter. They also suggest a threshold in both upper and lower limits of wave energy in kelp growth; i.e. the higher the wave energy the greater the production, but at the very intense levels found in shallow water offshore in winter, extensive damage and removal of the plants occurs. Observations in later winter, early spring bear this out (Gerard and Mann, 1982).

The growth of plants with larger fronds was in most cases significantly higher than in smaller frond plants (Table 5). Mann (1972b) found that the rate of increase in length was roughly the same in all size classes, but that the total number of new cells produced was greater in larger, older plants.

There was no evidence of mass mortality in the decrease of urchin abundance from summer - fall to late winter. We believe that the increase in wave turbulence throughout the winter months was accompanied by animal migration, either to deeper waters or into cavities in the rocky substrate and was the primary factor involved in the apparent population decrease.

Urchin grazing of kelp can be considerable (Table 8). Due to the lower numbers of urchins/m^2, the grazing rate is very much reduced in shallow water (2.5m) as compared to the 5.0 or 10.0m depths. The highest rate of consumption occurs at 5.0m in the exposed region. This region is also the zone of highest kelp productivity. Since cages were only placed in the outer bay region, it is unknown whether grazing rates vary in exposed and inner bay regions. Within the bay, summer grazing is reduced to roughly 50% of that in exposed areas, and in the winter there is a general reduction in grazing as compared to summer. In shallow water (2.5m) year round urchin consumption of kelp is approximately 7% of production, and while limited data are available for 10.0m, it would appear that consumption is even higher. It appears that the kelp forest is very much limited by grazing at its lower end in Maine waters, whereas increased wave action in shallower water limits the effect of urchins on kelp growth in those zones. Grazing limits the lower boundary of the kelp zone to a depth of 5-10m shallower than it would exist without grazing, thereby reducing the total potential kelp production by one-half. In larger bays (e.g. Penobscot, Bluehill, Frenchman) with considerably deeper hard substrate, urchin numbers are likely to be sufficient to graze up into the spring low tide zone. With these factors in mind, situations that might increase urchin grazing should be considered with regard to a general limiting of primary production on rocky coasts.

The investigation of Gouldsboro Bay’s outer rocky shores in late winter clearly demonstrated that much of the kelp biomass is eventually washed onto the shore. This process is shown graphically in figure 79 as a plot of "excess" (i.e. un-grazed) production as compared to standing crop. Independent of urchin grazing, kelp biomass is markedly reduced in late winter. Growth from April to August (at 15-40g(wet)/m^2/d) is capable of increasing biomass levels from the 1-4kg/m^2 levels at the end of

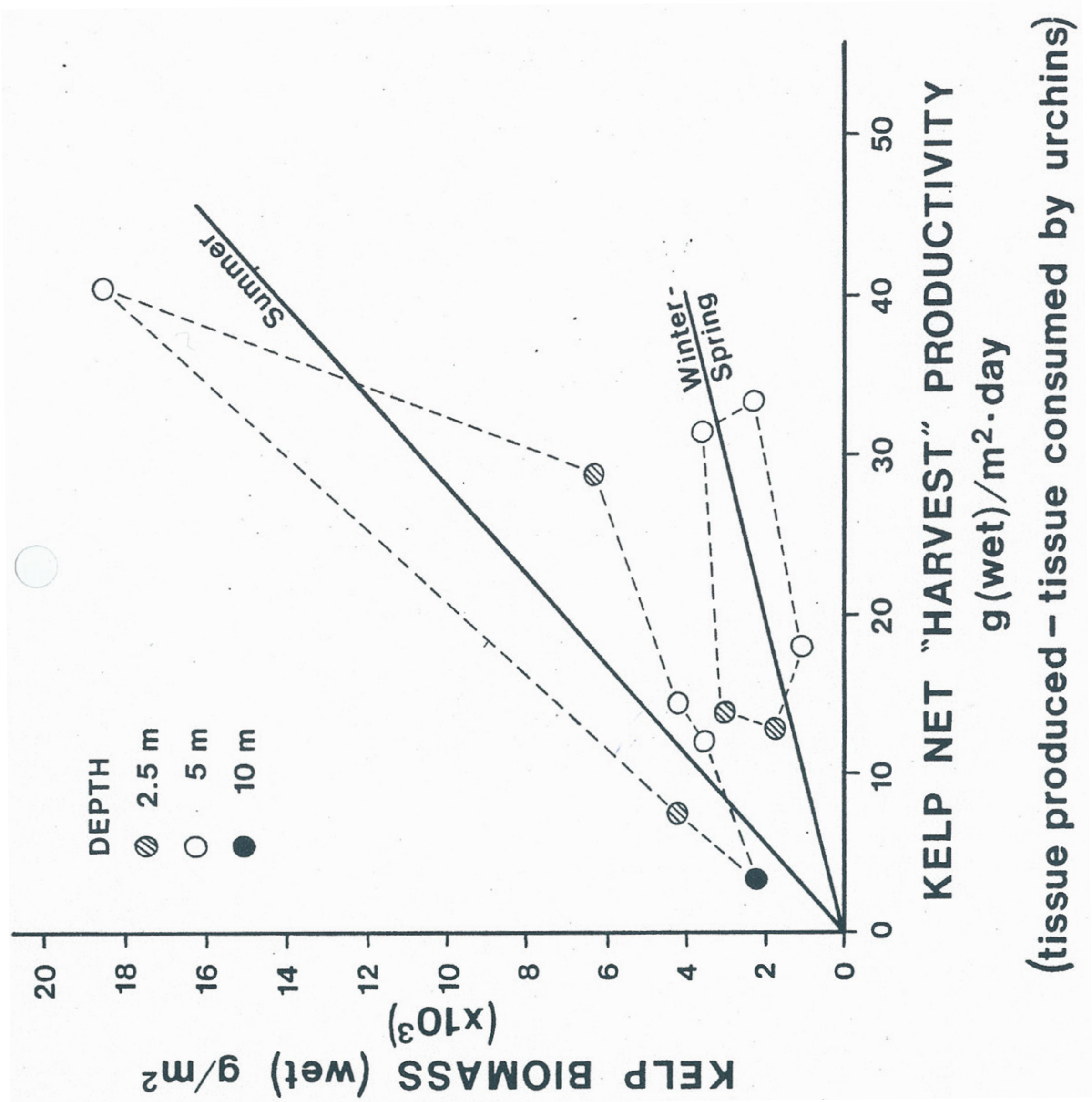


Figure 79. Kelp biomass by season and depth as a function of kelp production minus kelp grazed by sea urchins.

the winter to near peak summer levels of 2-7kg/m$^{2\cdot}$ In this respect, the 18.7kg/m^2 biomass found at 2.5m in the exposed region seems high. Given a later winter biomass of 4kg/m^2, a production rate of 100g/m^2/d, exclusive of urchin grazing, would be needed to develop 2kg/m^2 by late winter. It is possible that the winter of 1981-82 was characterized by relatively calm weather leading to less kelp dislodgement and high standing crop levels during the summer of 1982 when this data was collected.

In general, while losses in *Laminaria digitata* in winter can be considerable, the primary seasonal change in the kelp community is a change in abundance of *Laminaria longicruris. L. longicruris* shows considerably higher rates of production and winter losses than other species in the kelp forest. Even at 10.0m depth in the inshore region, where it has less than half the summer biomass of *Agarum cribrosum*, *L. longicruris* has roughly twice the productivity.

Based on the intensive studies carried out in this project, , it was determined that rates of kelp primary production are considerable in the Gouldsboro Bay area. Under optimum conditions, it approaches the highest rates of plant production known anywhere in the world. These coastal ecosystems are dynamic, with approximately 20% of production going to urchin grazing each year and most of the remainder being removed by winter wave action and delivered to the beach as drift.

Urchin grazing is a major factor in limiting kelp standing crop, and probably production as well, in deeper waters on exposed segments of the coast and in larger bays. In smaller bays and areas where protected shores have more gradual slopes, providing limited hard substrate with depth, both urchin grazing and kelp growth is probably limited due to lack of substrate. In these areas intertidal rockweed growth becomes the major form of primary production.

In the shallowest waters within Gouldsboro Bay and on the shallow portions of the rocky exposed coast outside the bay, urchins are limited by wave action and thus grazing has little effect on kelp production. Peak kelp production also appears to require considerable wave motion. Kelp production in exposed areas, depending upon season, reaches several times the levels achieved in protected sites. However, the intense wave action characterizing winter in exposed areas is damaging to kelp plants by removing a major part of the previous year's growth and delivering it to the beach.

Wave motion, particularly wave surge, is likely one of the most critical factors determining kelp production, just as it is for benthic production in general. There is little question that production is light limited, both winter and summer, however this effect is partially hidden by the overwhelming control of wave action. In the strong tidal situation of eastern Maine, we found no evidence of nutrient limitation.

Under conditions of moderately strong wave action, with summer peak light energy levels of 400-600 µE/m^2/sec, kelp productivities are around 10g(dry)/m^2/d. With winter peak light energy levels of 50-200 microE/m^2/sec, kelp productivities of 3-6g(dry)m^2/d are obtained. We suggest that in exposed to semi-exposed areas on the Maine coast, kelp production is limited only by wave action and available light. In more protected areas and in deeper water, production is limited by a lack of substrate, by urchin grazing and by the reduced effect of wave motion which may allow silt build-up on the kelp fronds.

Shelly and Armored Bottoms

In areas of strong current, restricted primarily to Eastern Way, at the mouth of the bay and off Rogers Point at the mouth of Joy Bay, fine sediments and silt are swept away by water turbulence and flow. Primary productivity is limited on these bottom types, as they are characterized by abundant pebbles, covered with coralline algae and by deposits of mollusc shells. Although an active area for sea scallops, armored bottoms are limited in area in Gouldsboro bay (Figure 53,73; Table 1). A related area, lying in a "wave shadow" of the islands, lies at the southwestern corner of the bay. Small, broken shells, particularly fragments of barnacles from the wave exposed islands at the mouth of the bay, collect in large quantity in this area. The sand dollar *Echinarachnius parma* is abundant on this bottom (Figure 80).

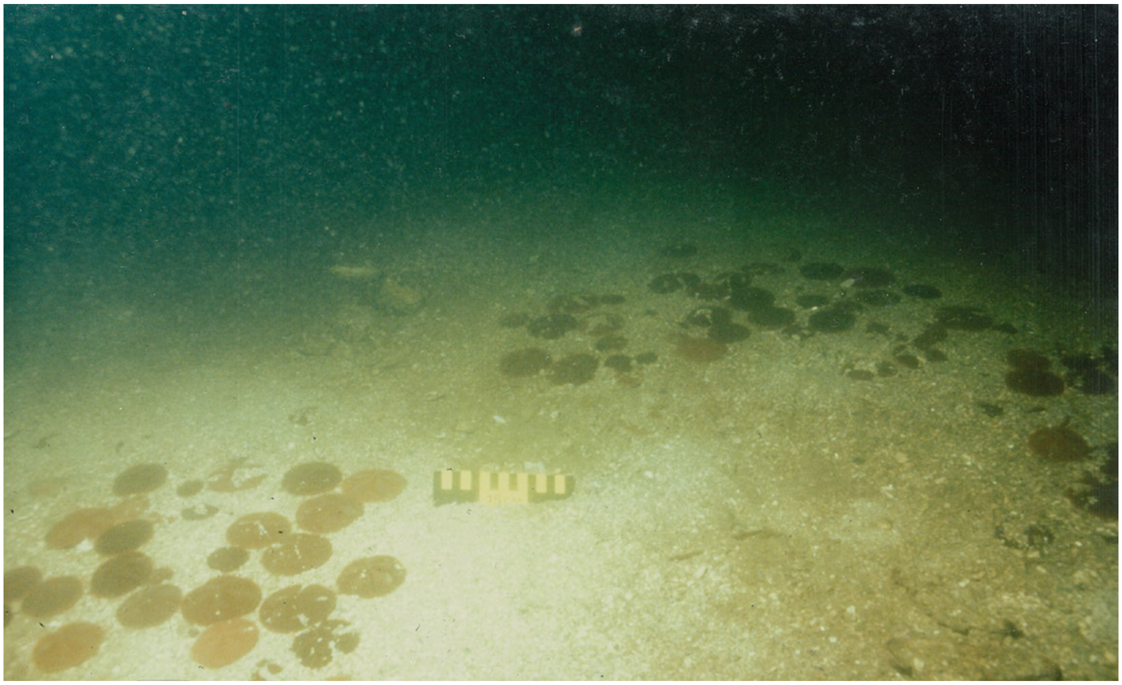


Figure 80. Echinarachnius parma (sand dollar) shell-hash community at 30 feet in the southwestern corner of the Bay.

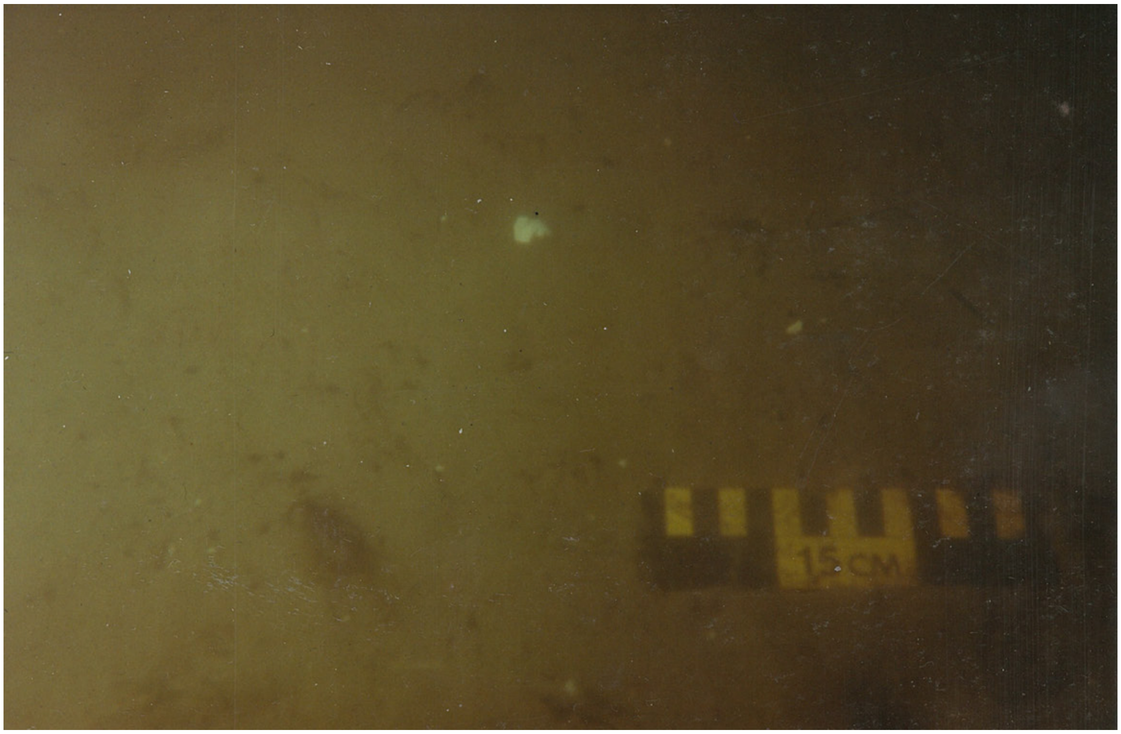


Figure 81. Silty mud community at 40 feet in the central part of the bay. The light brown haze on the surface is a diatom cover.

A very large part of the bay is occupied by a fine-grained, almost soupy mud, in the inner Bay, and a more sandy silt seaweed (Figure 81). This bottom has been cored and extensively grab sampled. The percentage of organic material in the bottom sediments increases from less then 2% near the mouth of the bay to 3-5% in the mid-upper bay, finally reaching 5 to over 10% in the mud flats. Since the primary source of that organic content in primary productivity lies in the mid and upper bay, dropping off markedly in Joy and West Bays, it seem highly likely that there is a shoreward transport and retention mechanism for fine organic materials as well as fine inorganic sediments.

Soft Bottoms

Soft bottoms of primarily sandy-silt with 10-30% clay size particles dominate much of Gouldsboro Bay and the off lying inshore waters (Figure 53). In the higher energy lower Bay and the deep portions of the close in inshore waters the sediments shift to silty-sand, where the wave or current energies are not sufficient to produce an armored bottom. Nevertheless, over much of the middle Bay and the deeper inshore waters, a rich soft bottom benthic infauna degrades the continuous supply of organic particulates derived from the breakdown of both macroalgal detritus and detritus from the plankton community. Some of the this infauna relies on filter feeding of the water column and some are in-situ predators; the majority of the infauna are deposit feeders.

The dominant species were defined by the collecting program (Tables 9-12). Ten to fifteen species of benthic macro-fauna occur on the mud flats, 20-30 species are present in the upper Bay, and 40-80 species characterize the outer Bay and inshore regions. A Bray-Curtis similarity analysis showed a strong, in-Bay, inshore, offshore set of groupings that are summarized in the tables for the dominant species. A total species count would require increasing the 6 - 9 stations per zone to about 10 -20 stations. The following is a preliminary biogeographic analysis of the benthic infauna.

As shown in Table 9, there is a group of wide-ranging species that occur throughout the bay subtidally. These species occur in all four zones, including offshore, often in great abundance.

With the exception of the circumpolor species *Mytilis edulis*, this group represents the dominant, benthic soft bottom fauna of the temperate/subarctic region of the Western Atlantic. There is no obvious tendency for a phyletic/geographic pattern of distribution in the Gouldsboro Bay area for any of the species; also, the mollusc/amphipod/polychaete ratio is about what it is for the fauna as a whole.

It is likely that there is an error in the identification of

Table 9

Wide ranging species of benthic macro-infauna

	North America	Europe (related species)
Nucula proxima	Maine to Florida	No (N. silcata)
Nucula delphinodonta	Labrador to New Jersey	No (N. tenuis, N. nudeus)
Mytilis edulis	S.Carolina-Circumpolar	to Mediterranean
Cerastoderma pinnulatum	Labrador to Cape Cod to North Carolina	No
Casco bigelowii	Maine to Block Island	No
Corophium volutator	? Maine	English Channel and North
Ninoe nigripes	Gulf St. Lawrence to Gulf of Mexico	No
Nephthys incisa	Arctic to Chesapeake	No (N. caeca, N. histricus, N. homergii)
Lumbrinereis tenuis	Bay Fundy to Florida	No (L. hibernica, L. impatiens)
Ophelina acuminata	Arctic to New Jersey	No
Mediomastis ambiseta	Maine to Delaware Bay	No
Aricidea catherinae	Maine to Block Island	No

Table 10
Intermediate ranging species of benthic macro-infauna

	North America	Europe (or related species)
Bay Group		
Ampelisca abdita	Gulf of Maine to Chesapeake Bay	No (A. brevicornis, A. diadema, A. macrocephalias
Leptocheiris pinguis	Labrador to Long Island Sound	No (L. pectinatus)
Cerebratulus locteus	Gulf of Maine to Chesapeake Bay	No (C. fuscus)
Tharyx acutus	Gulf of Maine to Delaware Bay	No (T. marioni)
Aglaophemus neotenus	Gulf of Maine ?	No
Scoloplos acutus	Arctic to Virginia	No (S. armiger)
Prionospio steenstrupi	Gulf of Maine to Texas	Reported in Scotland
Aricidea suecica	Gulf of Maine ?	No (A. Catherinae)
Nepthys ciliata	Arctic to Cape Cod	No (N. histricus, N. caeca, N. hombergii)
Outer Group		
Edotea montosa	Gulf of Maine	No
Sphenia sp.	Gulf of Maine ?	No (S. binghami)
Astarte undata	Gulf of Maine to Martha's Vineyard	No
Crenella decussata	Gulf of Maine to Long Island Sound	In Kattegat ? Elsewhere
Alvania carinata	Gulf of Maine to Martha's Vineyard	No (A. cancellata)
Periploma papyratium	Gulf of Maine to Martha's Vineyard	No
Diastylis quadrispinosa	Gulf of Maine to Block Island Sound	No (D. goodsiri D. rugosa D. laevis)

Table 11
Narrow ranging species of benthic macro-infauna

	North America	Europe (or related species)
Cyclocardia borealis	Labrador to Long Island	No
Diastylis polita	Maine to Martha's Vineyard	No (D. goodsiri)
Diastylis sculpta	Maine to Block Island Sound	No (D. rugosa D. laevis)
Eudorella pusilla	Maine to Block Island Sound	No (E. emarginata)
Harpinia propingua	Maine to Block Island Sound	No (H. antennaria)
Ochomonella minuta	Maine to Block Island Sound	No
Phoxocephalus holbolli	Maine to Block Island Sound	No
Ampharete acutifrons	Maine to Cape Cod Bay	Scotland (? Elsewhere)
Anaitides mucosa	Maine ?	No (A. maculata A. groenlandia)

Table 12
Outer group species of benthic macro-infauna
Lower Bay Stations

	North America	Europe (or related species)
Nuculana pernula	Gulf of Maine	No (N. minuta)
Dentalium entale	Gulf of Maine	English Channel to Kattegat
Thyasira flexuosa	Gulf of Maine to Long Island Sound	Abundant English Channel and North
Thyasira tris	Gulf of Maine	No (T. flexuosa)
Diastylis cornufer	Gulf of Maine	No (D. goodsiri D. rugosa D. laevis)
Terebellides stroemi	Gulf of Maine to Block Island Sound	Abundant English Channel and North
Trichobranchus glacialis	Gulf of Maine	Abundant English Channel and North
Ampharete arctica	Gulf of Maine to Block Island Sound	No (A. actifrons)
Maldane sarsi	Gulf of Maine	English Channel and North
Sternapsis scutata	Gulf of Maine to Martha’s Vineyard	English Channel and North

Corophium volutator. This species has apparently not been reliably identified on the east coast of North America and it is widespread in western Europe. An analysis of functional relationships and trophic structure in the benthic infauna is underway and is not reported at this time.

The species that are widespread and generally abundant in the Gouldsboro fauna, but tending to be distributed primarily offshore and in the lowermost Bay, are given in Table 10. Some of these species occur entirely within the lower Bay.

These species represent the lesser abundant and less widespread but still important elements of the temperate/subarctic region of the western North Atlantic. While there is a very strong tendency for molluscs to dominate the offshore and lowermost Bay and polychaetes to dominate the Bay, suggesting a feeding or substrate limitation that is phylum-related, the offshore /lower bay group tends to have a narrow geographic distribution (mostly Gulf of Maine to just south of Cape Cod) while the Bay group tends to be much more widespread (either Gulf of St. Lawrence or Labrador to Cape Cod or Gulf of Maine to the central coast and southwards. This suggests that the offshore/Bay pattern is also geographic rather than ecologic in nature.

The only two species of these groups that also occur in western Europe, *Prionospio steenstrupi* and *Cremella decussata* could represent identification problems. However, they are apparently not widespread in Europe, and thus remain poorly known. Except for *Mytilis edulis*, and three species with possible identification problems, the major widespread species of the Gouldsboro Bay fauna, worms, molluscs and amphipods, are all restricted to the western Atlantic.

Species that occur at low abundances but at relatively high frequencies restricted to specific parts of the Gouldsboro area are listed in table 11. These species occur at many or even most of the lower Bay stations generally in small numbers. In some cases abundances were high at one or two stations.

This group appears to represent the North Atlantic Subarctic element in the fauna, being largely limited in geographic distribution and in local (Gouldsboro) distribution. It is to be expected that many have a more northerly distribution and may be important but as yet unidentified from the Gulf of St. Lawrence.

Ampharete acutifrons is the only species reported from Europe. Since it appears to have a very limited distribution there (Scotland), the identification may well be in question.The species listed in table 12 occur at many or even most of the lower Bay stations, generally in small numbers. In some cases abundances were high at one or two stations.

In great contrast with all other groupings, over half of these species also occur in Europe. Most of this outer group of benthic infauna are amphi-Atlantic species, in continuing contrast with the multi-regional species. For the group, the phyletic balance is about the same as the benthic soft bottom fauna as a whole (in strong contrast to the bi-regional group). All of this strongly suggests that this is a largely a Boreal element, probably generally widespread in northwestern Europe and offshore northwestern North Atlantic, and tending to be important only where temperatures remain above 2-4°C in winter and below 12-15°C in summer.

Planktonic

Investigations of the phytoplankton, primarily diatoms, of Gouldsboro Bay (Figure 82) are underway and will be reported on at a later time. Primary productivity studies in the water column are discussed below. In this section we will briefly discuss our studies zooplankton populations.

Although our quantitative studies on Gouldsboro Bay zooplankton are relatively minimal, preliminary observations show the same basic generic percentages previously published for the Gulf of Maine (Sherman, 1963). Bigelow (1926) and Fish and Johnson (1937) also indicated that copepods were the most abundant and comprised the greatest volume of zooplankton occurring in inshore Gulf of Maine waters. These investigators also showed that volumes of these zooplankton were consistently higher west of Penobscot Bay than east of this region. However, while the copepods were the dominant group throughout the summer and early fall, the cladocerans, very abundant in early summer,

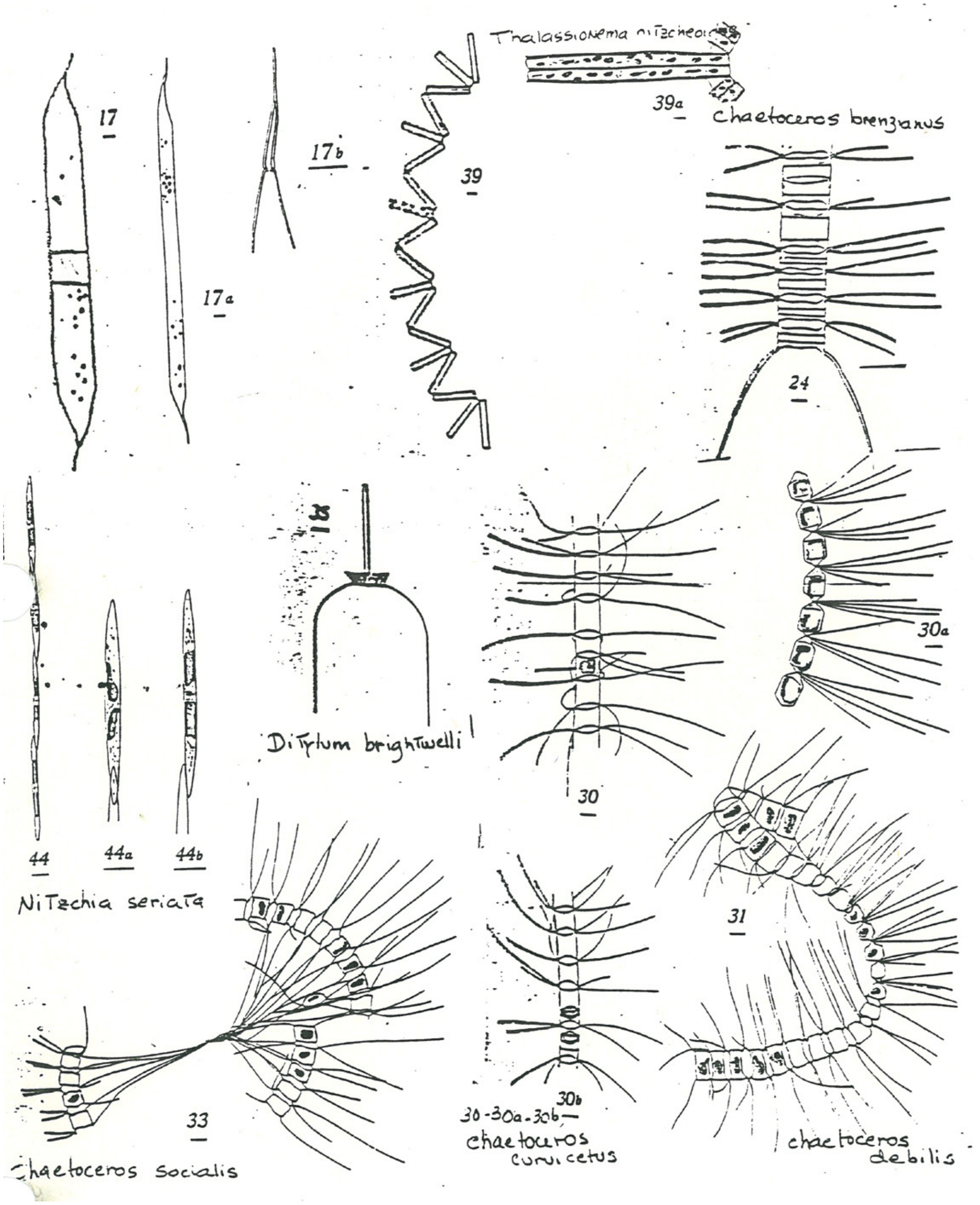
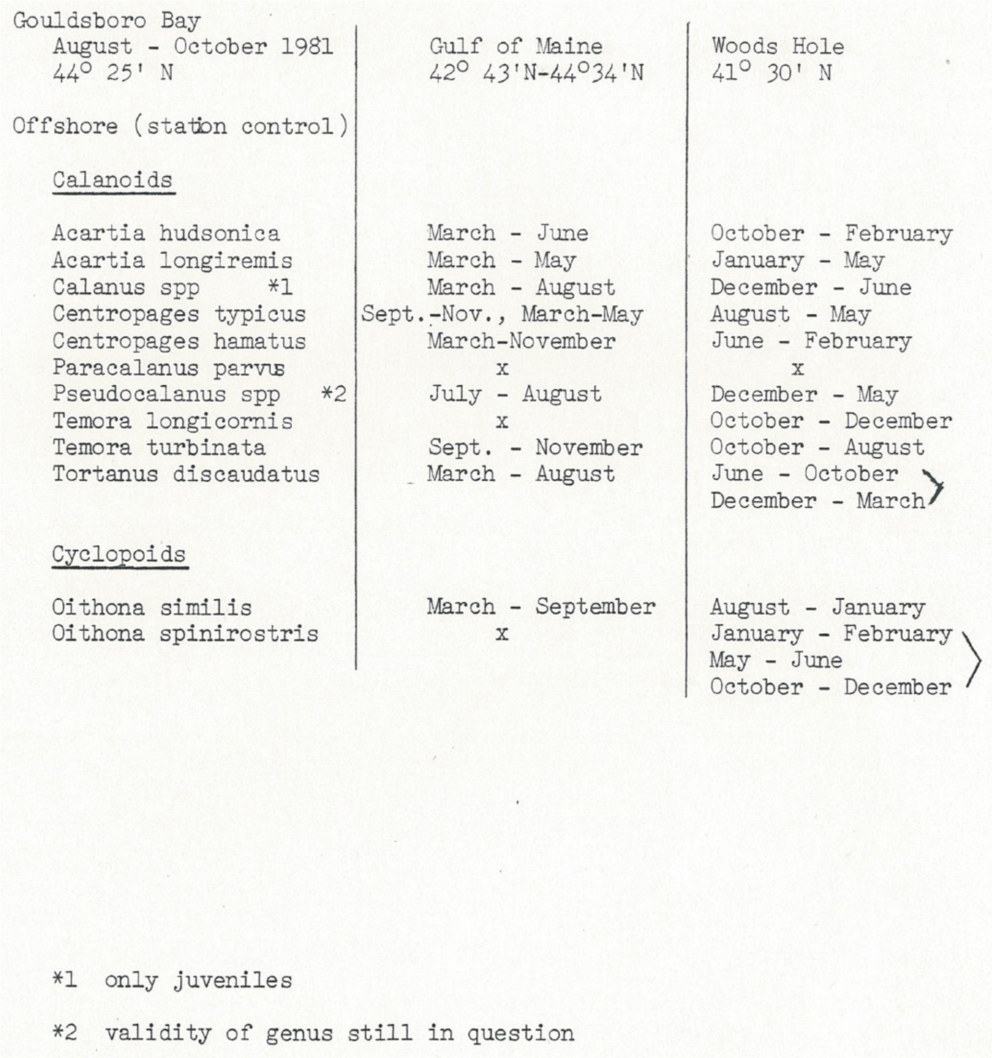


Figure 82. Dominant planktonic diatoms of inner Gouldsboro Bay.

decrease in numbers and are practically absent by early fall. The spring and summer decline in percentage composition of cladocerans is associated with the increase of other abundant zooplankton groups, particularly meroplankton. The abrupt rise in decapod larvae in spring and the eggs of many invertebrates during the summer indicate the breeding period of many invertebrate species during warmer months.

Although studies of zooplankton from a line of six stations extending up the axis of the bay were examined in this study, only the outer and inner most stations are compared and contrasted in this report (Tables 13, 14; Figures 83, 84).

The summer/fall zooplankton distribution in Gouldsboro Bay follows a typical estuarine pattern, despite only very minor temperature and salinity gradients, as discussed above. The community at the mouth of the bay is comprised of common shelf-dwelling copepods and the cladocerans *Evadne* and *Podon*. In the late summer of 1981, this was in agreement with oceanographic conditions, a salinity of 32,0% and a temperature of 13.5°C, typifying water north of Cape Cod. The presence of the cold water shelf *calanoids Pseudocalanus minutus, Paracalaus parvus, Tortanus discaudatus* and *Calanus* sp, quite near the mouth of the bay indicates limited mixing of shelf and bay communities. The cyclopoid *Oithona spinirostris* is an offshore warm water transient probably carried in form the Brown Bank areas, along the southwestern coast of Nova Scotia by the intrusion of oceanic

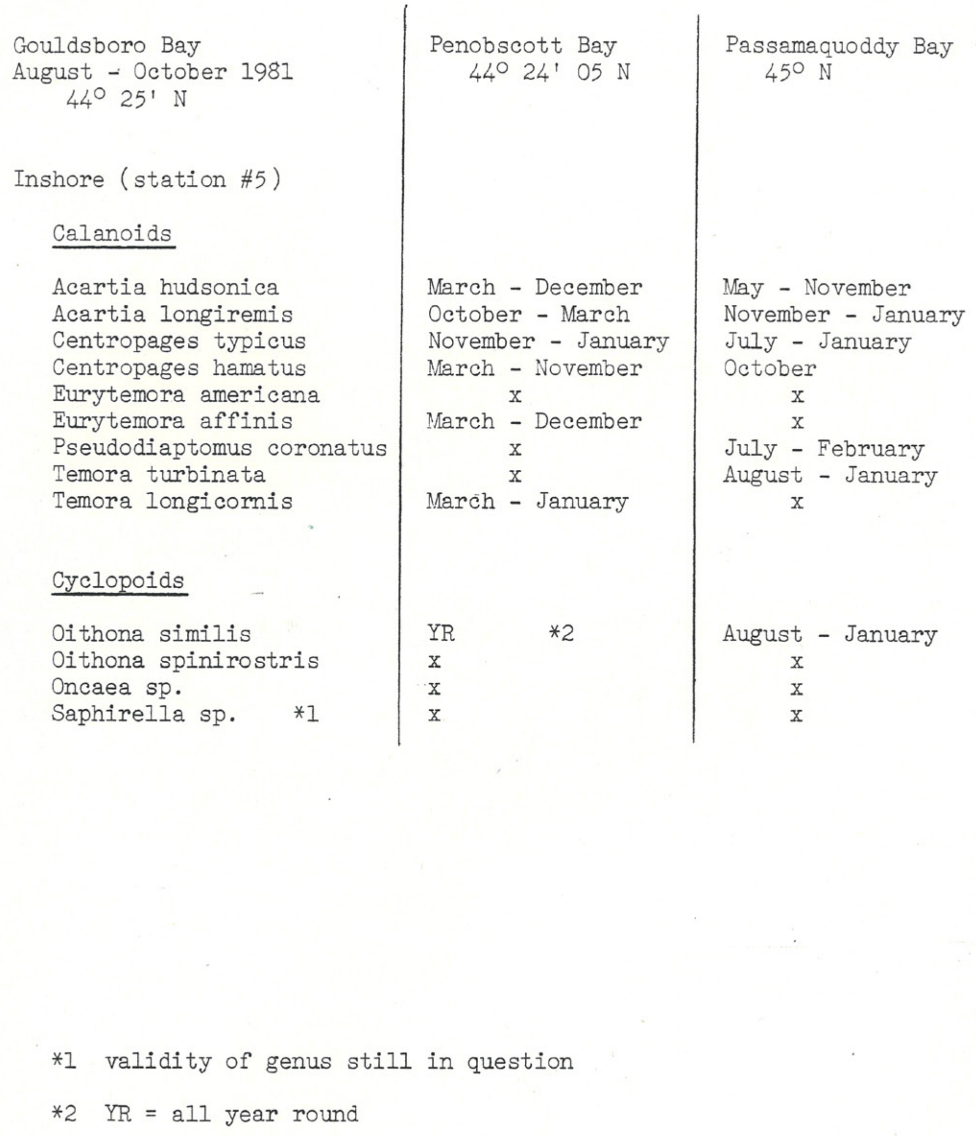


Gouldsboro Bay August - October 1981 44° 25' N	Gulf of Maine 42° 43'N-44°34'N	Woods Hole 41° 30' N
Offshore (station control)		
__Calanoids__		
Acartia hudsonica	March - June	October - February
Acartia longiremis	March - May	January - May
Calanus spp *1	March - August	December - June
Centropages typicus	Sept.-Nov., March-May	August - May
Centropages hamatus	March-November	June - February
Paracalanus parvus	x	x
Pseudocalanus spp *2	July - August	December - May
Temora longicornis	x	October - December
Temora turbinata	Sept. - November	October - August
Tortanus discaudatus	March - August	June - October December - March
__Cyclopoids__		
Oithona similis	March - September	August - January
Oithona spinirostris	x	January - February May - June October - December

*1 only juveniles

*2 validity of genus still in question

Table 13. Species of copepods occurring offshore Gouldsboro Bay and at other offshore northwestern Atlantic localities.



Gouldsboro Bay August - October 1981 44° 25' N	Penobscott Bay 44° 24' 05 N	Passamaquoddy Bay 45° N
Inshore (station #5)		
<u>Calanoids</u>		
Acartia hudsonica	March - December	May - November
Acartia longiremis	October - March	November - January
Centropages typicus	November - January	July - January
Centropages hamatus	March - November	October
Eurytemora americana	x	x
Eurytemora affinis	March - December	x
Pseudodiaptomus coronatus	x	July - February
Temora turbinata	x	August - January
Temora longicornis	March - January	x
<u>Cyclopoids</u>		
Oithona similis	YR *2	August - January
Oithona spinirostris	x	x
Oncaea sp.	x	x
Saphirella sp. *1	x	x

*1 validity of genus still in question

*2 YR = all year round

Table 14. Species of copepods occurring within Gouldsboro Bay and other Gulf of Maine bays

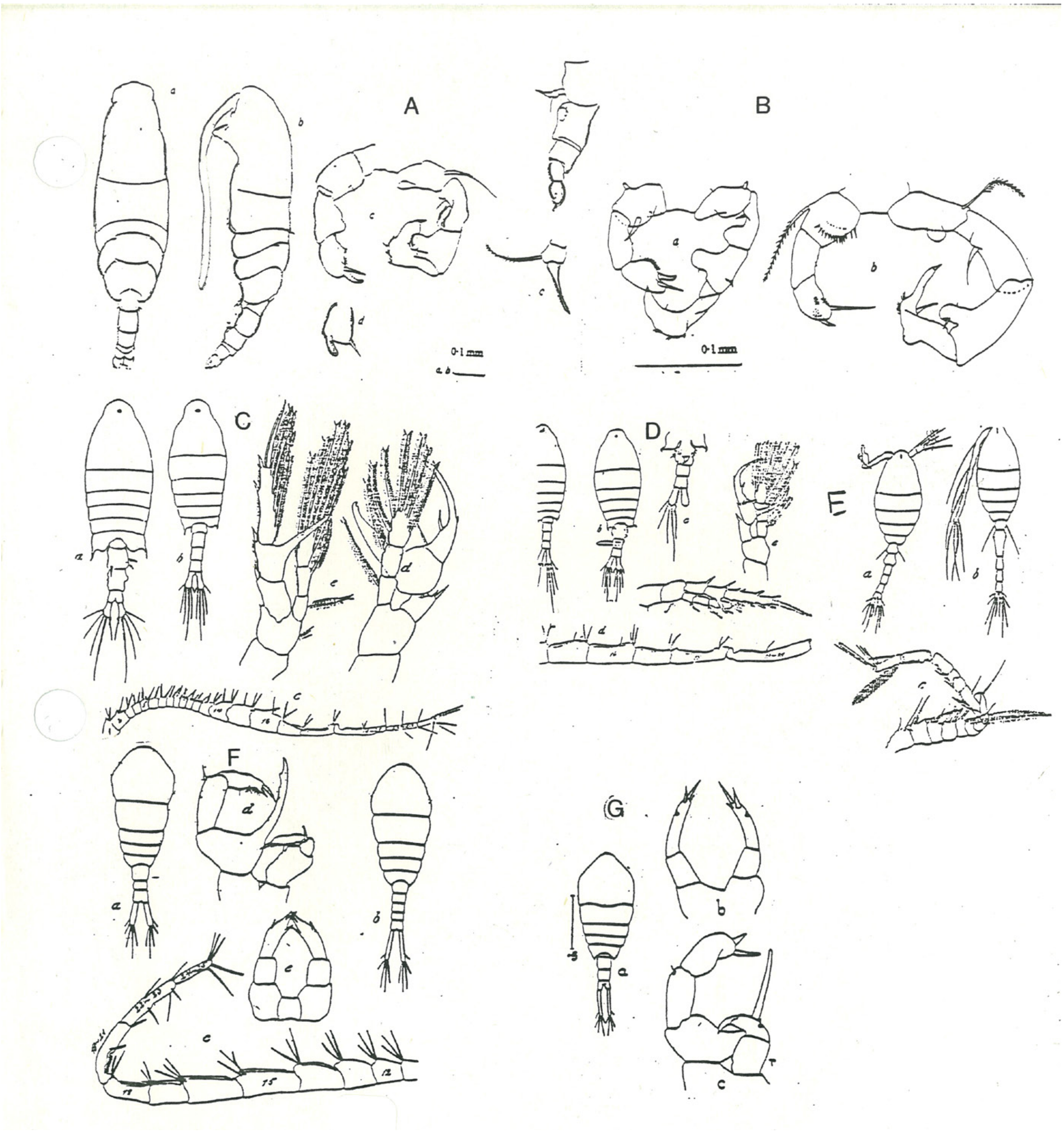


Figure 83. Copepods common to both Bay and Gulf of Maine waters.

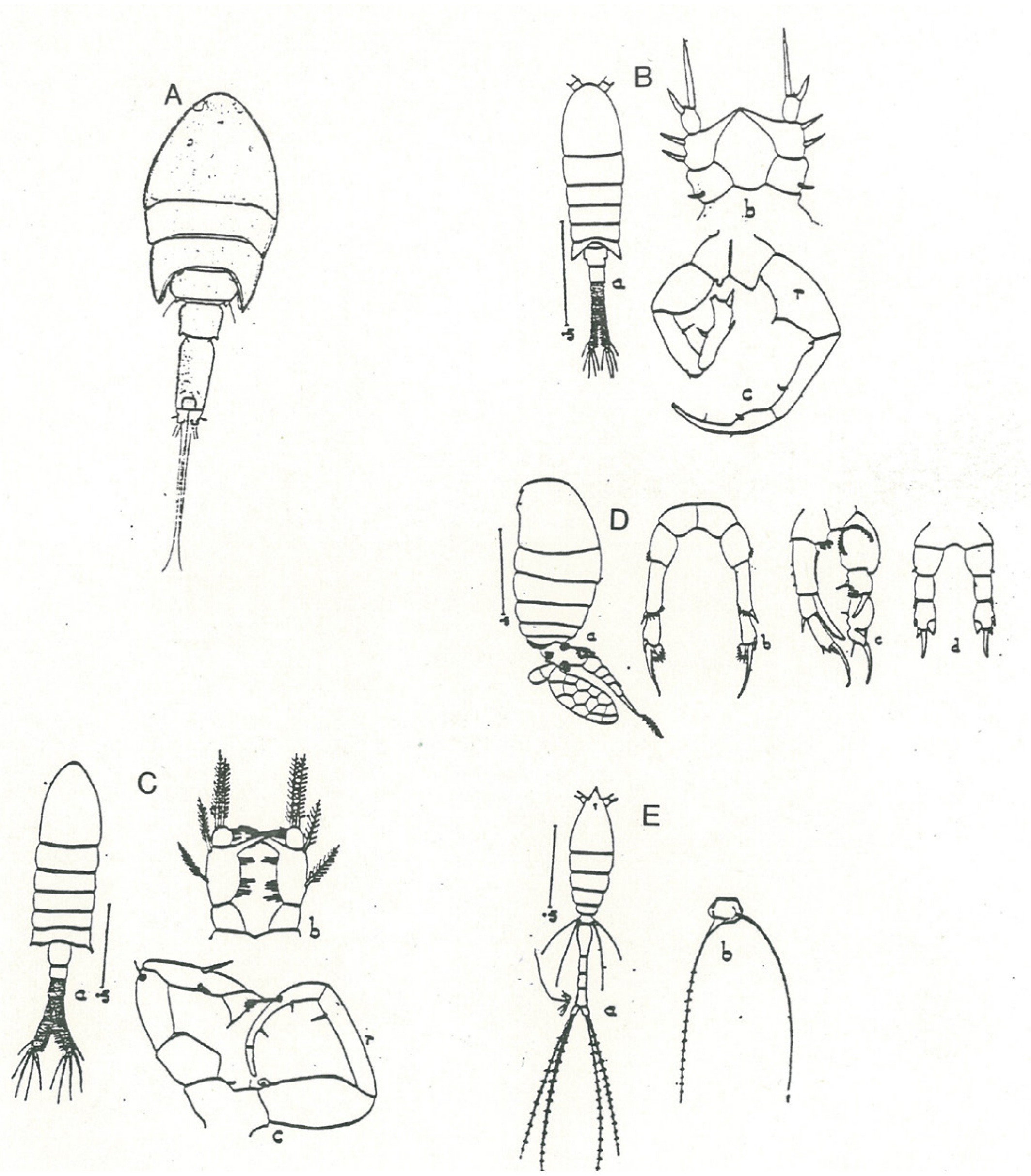


Figure 84A. Copepods occurring only within Bay waters of Gouldsboro Bay.

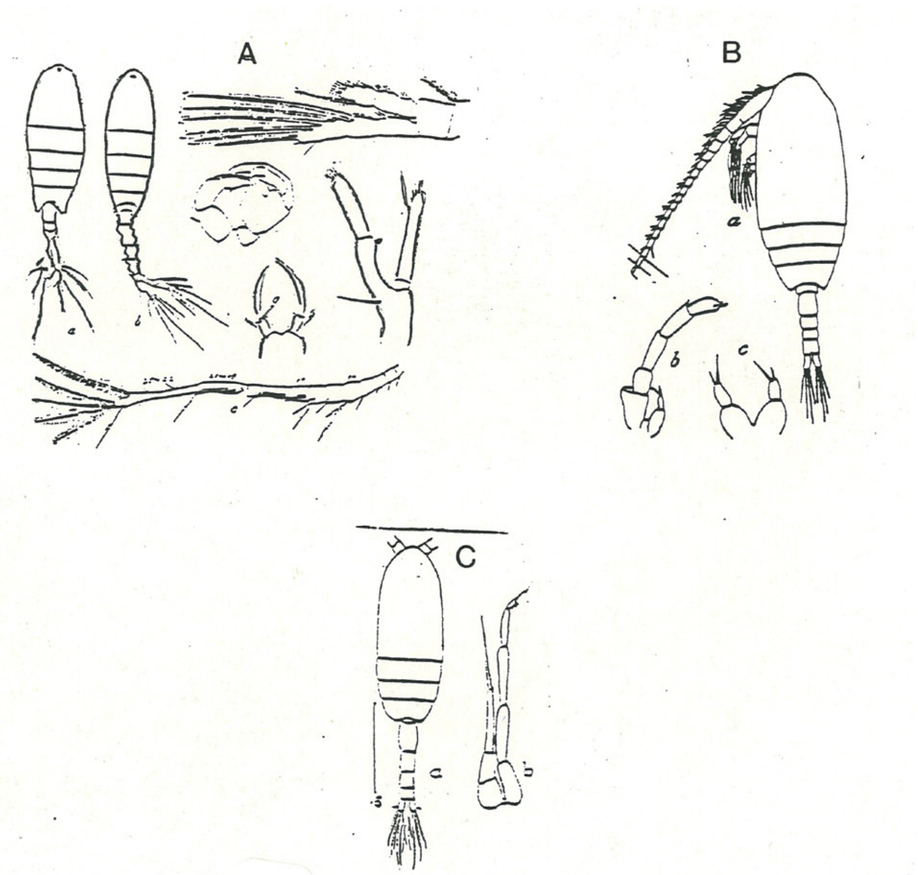


Figure 84B. Copepods occurring in inshore waters outside of Gouldsboro Bay, but not within the Bay.

water. It is not a typical member of the shelf community.

In addition to the seven species of copepods common to the offshore station, five species are unique to the upper stations of the bay. The *Euryhaline calanoids Eurytemora affinis, E. americana,* and *Pseudodiaptomus coronatus* are able to establish populations within the bay, possibly because they are not in direct competition with the shelf species, and they are able to survive the physical and chemical conditions of the Bay. Of the three cyclopoid species found in the bay, only *Oithona similis* is common at the offshore station. *Oncaea sp.* and *Saphirella sp.* are unique to the inshore stations.

Saphirella is of particular interest because the validity of the genus is still in question. The two pairs of unsegmented swimming legs instead of the usually five pairs, and the unsegmented abdomen, suggests immaturity. Yet these specimens lack the softness of the cuticle characteristic of juveniles. Nicholls (1944) suggests that *Saphirella* represents "the young form of *Hemicyclops*" due to similarity of the mouthparts. However, Gurney (1944) believes that this is unlikely due to the large size of most *Saphirella*. The specimens from Gouldsboro Bay average 1.5mm, and in normal free-swimming copepods the adult is about four times as long as the first copepodid stage. Most *Hemicyclops* do not exceed 1.5mm and it is unlikely that *Saphirella* could molt four times to the adult stage without increasing in size. In the most recent revision of *Hemicyclops*, Gooding (1960) states that a lack of information on the morphology of the larval stages in the family Clausidiidae prevents an adequate evaluation of Nicholl's suggestion. An investigation of the possible hosts of *Hemicyclops* is now underway in Gouldsboro Bay at a station where *Saphirella* is most abundant.

Examination of plankton samples from August to October showed some seasonal differences in both shelf and inner bay stations. From August to September, the stations near the mouth of the bay are dominated by juvenile copepods and adult cladocerans. The cladocerans are nearly absent in October collections and are replaced by adult copepods. These adults will remain in the plankton until they become reproductively active the following spring. The inshore samples collected in August, in addition to juvenile copepods and cladocerans, contain a wide variety of invertebrate larvae. Larval clams, snails, polychaete worms and decapod crustaceans suggest that Gouldsboro Bay serves as a nursery ground during the summer months. Whether this feature is part of the reproductive biology of the species in question (e.g., temperatures 2-4°C higher in summer may accelerate development; the greater abundance of organic detritus may provide more food) or is incidental to hydrographic factors forcing retention is as yet unknown. Samples taken in October are dominated by adult copepods, the breeding season having ended for most invertebrates.

The depletion of phytoplankton by zooplankton grazing during the late spring and summer is a common phenomenon in marine waters (Raymont, 1963) and probably is an important factor contributing to the growth of several species of zooplankton. However, grazing cannot be held completely responsible for the decrease on phytoplankton biomass, since the development of copepods follows the peak of phytoplankton production with a time lag of about 2 - 3 months (Margalef, 1963).

The nutritive values of diatoms and dinoflagellates are generally high and are considered to be the most important food for herbivorous and omnivorous copepods (Ankaru, 1963). However, preliminary observations on the phytoplankton standing crop in Gouldsboro Bay show that these organisms are neither very diverse nor abundant. This has led to the hypothesis that the large herbivorous zooplankton community must be feeding mostly upon nonliving particulate organics in the water column, possibly on the breakdown products of drift macroalgae, the most abundant organic source in bay waters. The concentration of bacteria in the water column would not be high enough to cover the demand of copepods, and since bacteria are not big enough to be retained by the collecting apparatus, they seem not to be significant as a direct food source. However, they may well be important secondarily in their attachment to organic particulates that are large enough for capture.

It has not yet been determined whether detritus is used effectively by herbivorous copepods as food. However, smaller planktonic animals are certainly important for predatory and omnivorous copepods. An attempt to establish a rough "food chain" per station is being carried out by observing the feeding habits of the zooplankton. According to Anraku and Omori (1963) there is a close relationship between the mouth parts and the feeding habits of copepods. In herbivorous species, the maxillipeds, second antennae mandibular palps and first maxillae are well developed to produce a pair of "feeding swirls". In predatory species, the mouth parts have few setae. The first maxillae, second maxillae and maxillipeds are modified as prehensile appendages. The cutting edges of the mandibles have very sharp teeth. In omnivores, these appendages have a structure intermediate between those of the two previous types.

The Bay stations (Figure 84a) are dominated by typical filter feeding "herbivorous" copepods rather than the more aggressive predatory animals. Filter feeders vibrate their mouth parts to set up feeding currents, using setae to strain diatoms, small invertebrates larvae, and perhaps organic particulates from the water. Most filter feeders found in Gouldsboro Bay are omnivores, but some species, such as *Centropages sp.*, are currently carnivores(Anraku and Omori, 1963). They most likely switch to herbivory only when invertebrate larvae are unavailable.

Acartia spp. use their second maxillae to rake the water rather than setting up feeding currents. Conover (1956) suggests that *Acartia* is unable to complete with efficient filter feeders and is basically confined to inner areas of bays and estuaries where phytoplankton and small animals (invertebrate larvae) are more abundant.

The stations outside the Bay (Figure 84b) show a significant reduction in the population of *Acartia*. The more carnivorous *Centropages spp*. and *Pseudocalanus spp*. are the dominant animals. *Tortanus discaudatus* is found only here. *Tortanus* is a large predatory copepod that has abandoned all methods of filter feeding. The mouth parts of these animals are characterized by a reduced number of setae and the presence of large spines for spearing prey. *Tortanus discaudatus* is known to eat adult copepods such as *Temora longicornis* and *Pseudocalanus spp*., as well as members of its own species (Anraku and Omari 1963).

As discussed below, planktonic primary productivity markedly decreases from the mouth to the inner reaches of the bay. This feature does not correlate with the corresponding decrease of filter feeding plankters into the bay and further suggests the importance of organic particulate feeding.

Nektonic

Herring are critical to the bay. They are fished from three weirs and the landings are discussed under utilization and treated in the preliminary systems analysis. Nevertheless, as near as we can determine at this time, Gouldsboro Bay is and has been traditionally a poor bay for herring. During the summer, a large breeding colony (100-150 animals) of the harbor sea *Phoca vitulina* occupies the ledges between Gouldsboro and West Bays. Seals are frequently seen in bay water at all seasons of the year. A relationship between the seal colony and the poor herring fishery, as well as the general lack of other finfish in the bay, as discussed below, is inferred but cannot be established at this time.

Although no formal analysis of finfish has yet been undertaken, it is quite apparent that the numbers and impact of these organisms (other than herring) is minimal in Gouldsboro Bay.

PRIMARY PRODUCTIVITY

Primary productivity and food webs in the ocean have been extensively studied, especially. with regard to the output of the ocean's major fisheries. Most fisheries are based on plankton production and although the actual level of phytoplankton production are under dispute (e.g., Kerwin, 1982), it is thought to range from about 0.1-2.0g(dry)/m^2/day. Ryther (1959) predicted that given optimal factors (particularly nutrient supply, extensive mixing and full tropical light utilization) a plant production rate of about 25g(dry)/m^2/day could be achieved. This level has been demonstrated (and exceeded) in fully mixed planktonic cultures (e.g., Spectorova et al, 1981).

It is believed that the productivity of benthic communities can be much higher than plankton communities, particularly on a yearly basis (e.g. Ryther, 1959), although relatively little effort has been put into examining the contribution of benthic communities to coastal food webs (see Mann, 1972). Many studies have concentrated on growth rather than productivity (e.g. Parke, 1948; John, 1982) or in the effect of nitrogen availability upon growth (e.g., Harlin, 1978; Gagne,1982). Based on the work of Ryther (1959),and assuming that light is providing the only limit to benthic production, one could predict that yearly primary production rates of at least 2-8g(dry)/m^2/day are possible at 40-50 degrees of latitude. The estimate would seem to confirm the discussion above where intertidal production rates of rockweed of

40-60g(wet)/m^2/day (approximately 8-12g(dry)/m^2/day) were demonstrated.

The Maine Coast is characterized by an extensive shoreline (3800 miles per 250 linear miles of coast); most of it is rocky and suitable for larger benthic algae. In this study we have chosen a more or less typical Maine bay with the intention of examining primary production under the varying conditions of "inner bay", "outer bay" and "exposed" environments to seek information that may allow rational estimates of primary production in the entire Maine coast.

Benthic Productivity

The primary productivity of the major benthic communities in the photic zone of Gouldsboro Bay was determined by measurements of biomass increase in the dominant plants of those communities. Comparative measurements were also carried out by determining the quantity of chlorophylls and accessory pigments per square meter in each community.

The quantity of chlorophyll and accessory pigments for each community was determined by sampling macroalgae and *Zostera* from a wide variety of local environments and analyzing them by calorimetric methods. Using the biomass data discussed above we were then able to calculate a mean photosynthetic pigment content per square meter for each community. These data are presented in table 15, along with a relative photosynthetic quotient based on

Table 15. Chlorophyll concentrations and estimated primary productivity for Gouldsboro Bay biological communities.

Community	(m^2 x 10^6 Area	(m) Mean Depth	(g) Pigment/ g/m^2	($uE/m^2/sec$) Light	(g x 10^6) Total Community Pigment	Proportional Productivity Light x Pigment	Community (%) Productivity
Intertidal							
Rocky	1.9	2	11.7	1200	22.2	1 (26640)	65.9
Mud Flat	3.5	2	1.5	1200	5.2	0.2	13.2
Subtidal							
Rocky	0.5	5	15.2	900	7.6	0.26	17.1
Zostera	0.7	5	2.3	900	1.6	0.05	3.3
Planktonic	14	4	0.014	850	0.2	0.0064	0.4
							99.9

light energy and pigment.

For macroalgal dominated communities, the percentages of total bay productivity provided by each community based on photosynthetic pigment is likely a reasonable estimate. Per unit quantity of pigment, planktonic cells are probably more efficient than macroalgae, and the primary productivity percentages for the plankton may be low. However, they are in rather close agreement with that reported for offshore areas in the Gulf of Maine by Reilly et al (1978).

Intertidally, *Ascophyllum nodosum* is the dominant plant on rocky bottoms. Its productivity was determined by counting the number of growing tips per square meter and measuring mean yearly elongation rates per tip. As we discussed above, branches of *Ascophyllum* produce one bladder per year and by cutting segments out and weighing them, a net yearly increase can be calculated. At each intertidal station, 75 yearly growth segments were weighed. Total rocky intertidal productivity was calculated by multiplying mean tip increase weight by the number of tips per square meter and then by the number of square meters of rocky shore in the bay.

Mud flat productivity was determined by measuring the standing crop of *Zostera* late in the season. In both the rocky and muddy intertidal, these are both minimum and net values, since they do not account for loss of whole plants during the summer in *Zostera* and the loss of branches on *Ascophyllum* during the spring and early summer.

Subtidally, kelp production was determined by direct measurement of frond elongation, determining mean increase per weight of standing crop and then by multiplying kelp bottom area by this value. Subtidal *Zostera* beds, being made up dominantly of plants several years old and occurring at shallow depth were assumed to have productivities equivalent to mud flat plants. This needs to be confirmed by direct measurement. These data are given in table 15.

Planktonic Productivity

Six stations were established in August and September along the axis of Gouldsboro and West Bays to determine factors relating to the planktonic primary productivity of Gouldsboro system (Figure 85). Nutrient, light and standing crop data were collected in addition to C^{14} productivity (Table 16). The relative contribution of plankton to the primary productivity of the Bay complex was estimated based on area and concentration of chlorophyll A in the water column.

Primary productivity was measured by the method first described by Steeman and Nielson (1952). Depth profiles were tested at five meter intervals at the deeper stations and shorter intervals where water depth was less than eight meters. Two dark bottles were included in each station. Samples were collected from depth with a Niskin sampler. placed in 300ml BOD bottles,

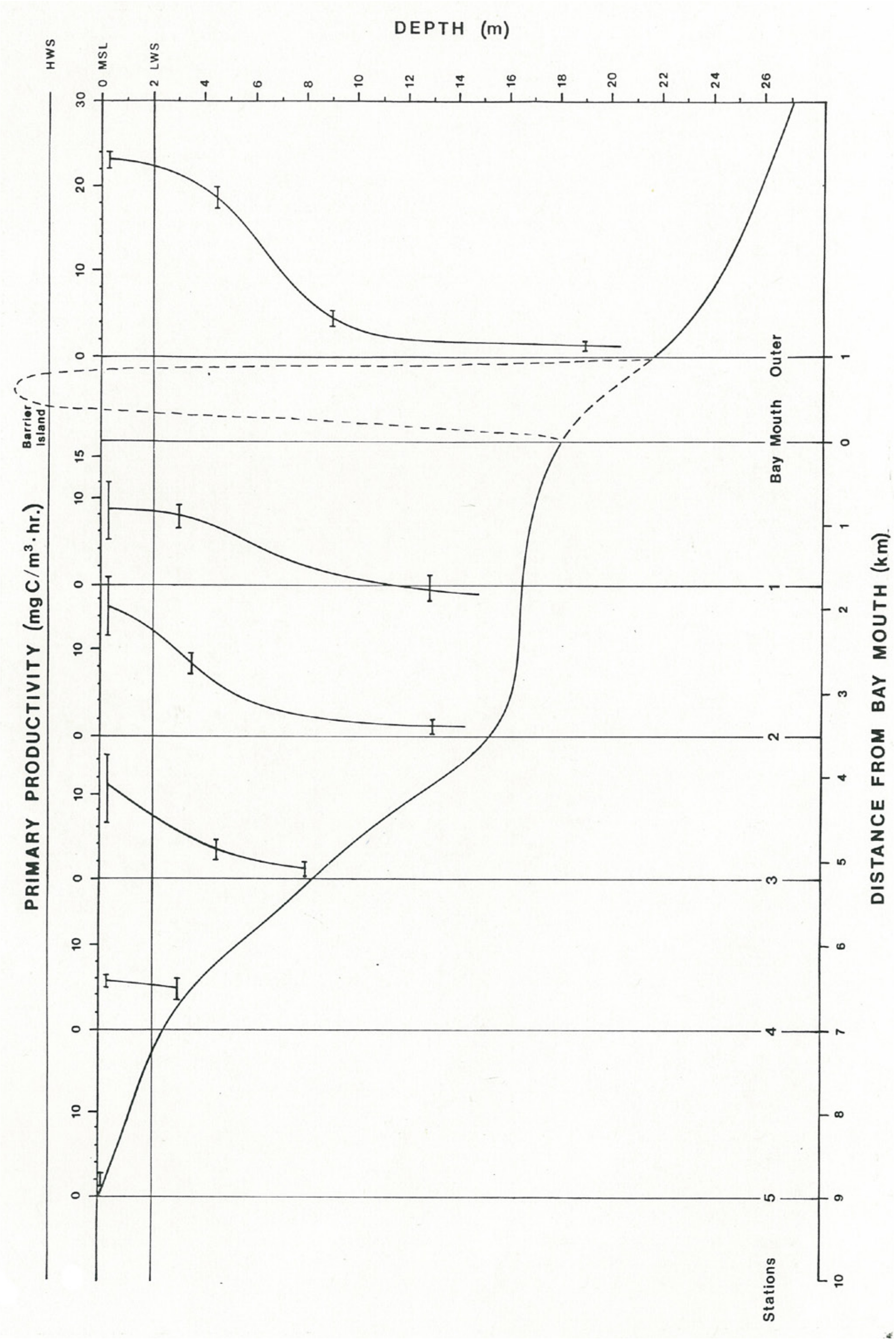
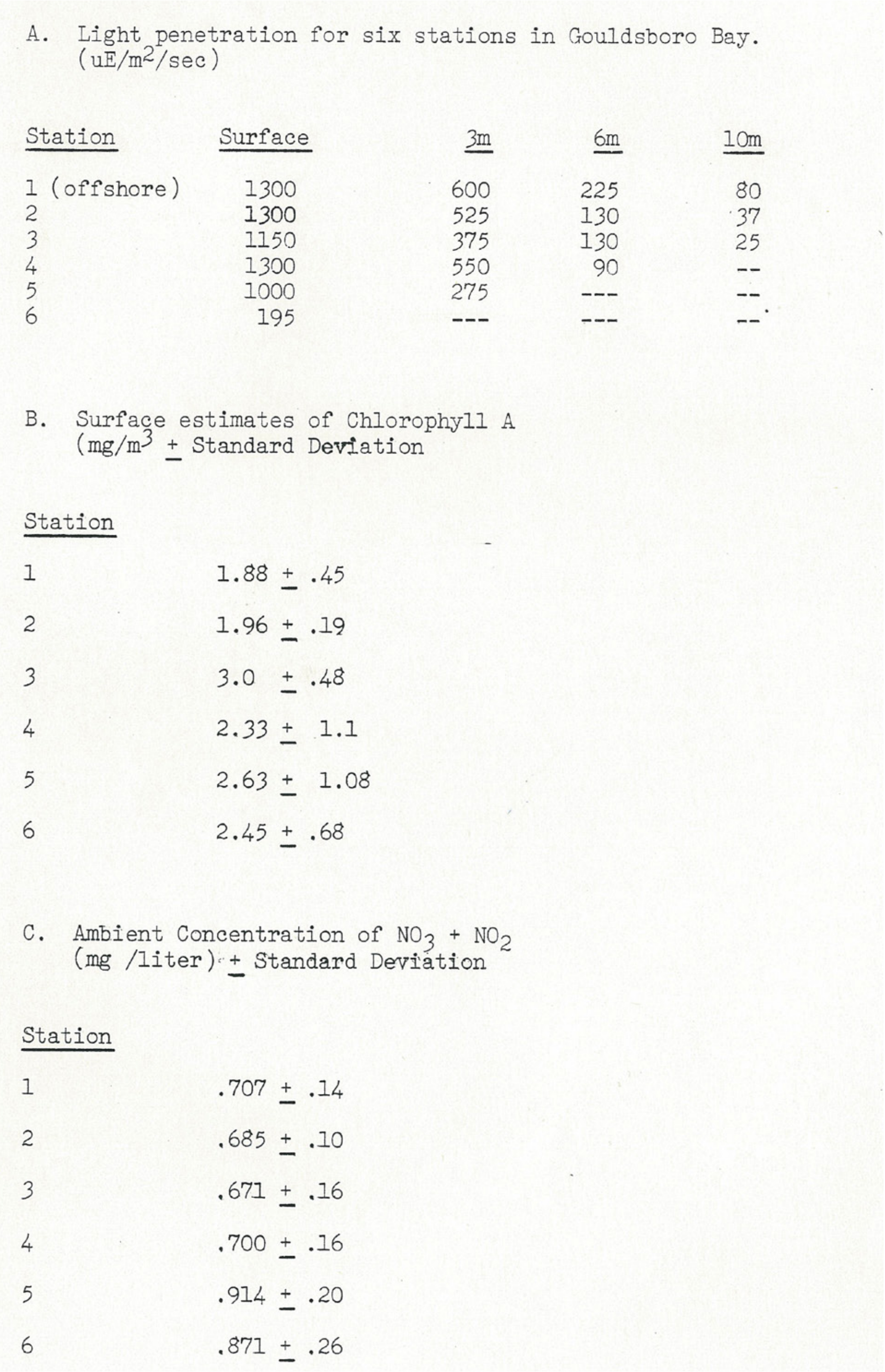


Figure 85. Planktonic primary productivity of Gouldsboro Bay

Table 16. Light penetration, Chlorophyll A concentrations and reactive nitrogen levels in Gouldsboro Bay.



A. Light penetration for six stations in Gouldsboro Bay.
(uE/m^2/sec)

Station	Surface	3m	6m	10m
1 (offshore)	1300	600	225	80
2	1300	525	130	37
3	1150	375	130	25
4	1300	550	90	--
5	1000	275	---	--
6	195	---	---	--

B. Surface estimates of Chlorophyll A
(mg/m^3 ± Standard Deviation

Station	
1	1.88 ± .45
2	1.96 ± .19
3	3.0 ± .48
4	2.33 ± 1.1
5	2.63 ± 1.08
6	2.45 ± .68

C. Ambient Concentration of NO$_3$ + NO$_2$
(mg /liter) ± Standard Deviation

Station	
1	.707 ± .14
2	.685 ± .10
3	.671 ± .16
4	.700 ± .16
5	.914 ± .20
6	.871 ± .26

inoculated with 2.5 uci/bottle of NA $HC^{14}O_3$, sealed and returned to the depths from which they were collected. Incubations were done between 1200 and 1400 hours on consecutive days. After two hours of incubation time bottles were fixed and subsamples of 50 and 150 mls were filtered, rinsed and stored in scintillation vials. Filter membranes were 2 micron acropore membranes. Samples were counted for C^{14} bete emissions on a Packard 2660 scintillation counter at he Smithsonian Radiation Biology Laboratory. Net productivity is reported as the difference between light and dark uptake.

Primary productivity generally increases from the head to the mouth of the bay system (Figure 85). Turbidity remains relatively constant inside the bay (Table 16a). It increases towards the mud flats and decreases offshore as expected. Chlorophyll measurements were made on different days from productivity but at the same stations; they do not reflect primary productivity (Table 12). The reasons for this are not clear. It is possible that prevailing tides or currents concentrate plankton in the upper reaches of the bay where they eventually sink out of the water column due to lack of mixing. Inner bay stations are probably not significantly different in light penetration, standing crop, or nutrients (Table 16). Primary productivity clearly increases in the direction of the open sea; this is probably partly due to mixing from waves and currents which are higher toward the mouth of the system and to decreasing turbidity.

Contributions of the phytoplankton to the primary productivity of the bay system may be assessed by combining an estimate for the euphotic area of the bay with an estimation of productivity per unit area. Within the Bay the photic zone is estimated to be not more than nine meters on an average day. Mean productivity has been calculated by breaking the bay up into five productivity areas, based on figure 85 and then into unit 3 meter depth zones, depending upon depth for each area. The mean value for midday at 28.1mgC/m^2/hour is considerably less then the productivity that is achieved just outside the bay (156mgC/m^2/hour - Figure 85). Mean bay productivity for the whole day would be about 0.7 for a 10 hour day of approximately 0.20gC/m^2/day. We assumed that August and September, in these moderate nutrient waters, should provide about an average planktonic productivity for the warm season. Assuming nil production in mid-winter, the average plankton production for the year would be about 36.5gC/m^2/year. This is well below the estimate of 150gC/m^2/year provided by the fish and Wildlife Service (1980). However, if the productivity values just outside the Bay are used, then one finds a yearly rate of 198gC/m^2/year. Clearly, geography and turbidity are very critical factors controlling planktonic productivity. Conversion of gC to wet biomass by a standard factor of 10 gives approximately 0.36kg(wet)/m^2/year, which is used in table 17 to calculate

Table 17. Area, plant biomass and primary productivity of the major biological communities of Gouldsboro Bay.

Area, plant biomass and primary productivity of the major biological communities of Gouldsboro Bay

Community	(X10^6 m^2) Area	(kg/m^2) Mean Standing Crop	(10^6 kg) Total Standing Crop	(kg/m^2 yr.) Mean Primary Productivity	(kg/yr.10^6 Total Community Primary Prod.	% of Total Bay
Intertidal						
Rocky	1.94	18.9	35.3	10.6	20.1	62.8
Mud Flat (m/w)	3.50	1.2 (on about one-half of surface)	2.1	1.2	2.1	6.6
Subtidal						
Rocky	0.56	5.8	3.2	7.2	4.0	12.5
Zostera soft bottom	0.68	1.56	1.1	(1.2?)	0.8	2.5
Planktonic	14.0	0.12	1.7	0.36	5.0	15.6
	20.68			X = 1.5 kg/m^2. yr	32.0	100

community productivity.

Total Bay Primary Productivity

Comparing community productivities calculated by photosynthetic pigment analysis (Table 15) against harvest and C^{14} analysis (Table 17) shows that, for macroalgae, the results are more or less in agreement. As mentioned above, chlorophyll probably gives a low value for the phytoplankton and the C^{14} value is probably closer to reality. In any case, it is quite apparent that within the bay system, benthic primary productivity dominates heavily over planktonic productivity. This is a factor of critical concern in any systems or management analysis, and has not been adequately assessed relative to the productivity of the entire Gulf of Maine system.

BAY UTILIZATION - FISHERIES

It is difficult to estimate the fisheries harvest from Gouldsboro Bay from the Maine Department of Maine resources and National Maine Fisheries Service data. These data are by county or sometimes township. Unfortunately, the bay forms the boundary between Hancock and Washington Counties, and the towns of Gouldsboro and Stueben also split the Bay. Nevertheless, the field biologists of both those Services were extremely helpful, and the data provided served to give us a larger scale framework into which a local analysis could be placed and judged.

The primary data presented here were derived from interviews with individual fisherman, processors and dealers and from formal reports being developed by local wardens and regional biologists. The study is incomplete at this time.

Table 18 establishes the basic fisheries patterns for the Maine Coast in 1980. Lobsters, scallops, clams and herring, in that order, are dominant in dollar value. However, in pounds landed, superficially the critical factor in a systems analysis, herring exceed all others by five times. In an individual bay environment, however, the situation is much more complex. As discussed below, an estimate of 650,000 pounds of herring were landed from Gouldsboro Bay in 1980 and 1981 as opposed to approximately 100,000 pounds (for two years) of lobster. Herring spend only a small part of their life cycle in the bay environment, and their occupancy in Gouldsboro Bay is sporadic. They feed on zooplankton and invertebrate larvae and are thus relatively low on the food chain. The herring fishery probably has little effect on the bay ecosystem. Lobsters, on the other hand are predators, and at least as adults, are probably the top carnivores in their own environment. Also, they spend a major part of their life cycle in bay waters. The effect of lobster fishing on the bay system is probably very marked. On the other hand, several times the weight of lobster removed from Gouldsboro Bay is returned to the bay in the form of lobster bait (herring and redfish), and the effect of this input needs to be carefully

Table 18. 1980 Maine landings of species valued at more than $50,000.

1980 Maine Landings* of Species Valued at More Than $50,000 Ordered by Descending Value with Poundage and Price per Pound Ranking.

Species	Rank	Thousands of Dollars	Percent of Total	Rank	Thousands of Pounds	Percent of Total	Rank	Dollars per Pound
Lobsters	1	41,705	45	2	21,981	9	5	1.90
Scallop, Meats	2	10,752	12	12	3,233	1	2	3.33
Clams, Soft, Meats	3	8,554	9	10	5,676	2	8	1.51
Herring, Sea	4	5,977	6	1	107,823	44	30	.05
Dab	5	4,914	5	4	14,553	6	14	.34
Ocean Perch	6	3,032	3	5	13,805	6	19	.22
Haddock	7	2,902	3	8	7,107	3	13	.41
Cod	8	2,623	3	7	11,359	5	18	.23
Pollock	9	2,094	2	6	12,855	5	22	.16
Gray Sole	10	1,900	2	11	3,601	1	12	.53
Bloodworms	11	1,404	2	28	118[a]	–[b]	1	11.90
Swordfish	12	1,190	1	22	584	–	4	2.04
Sandworms	13	1,095	1	26	354[a]	–	3	3.09
White Hake	14	844	1	9	5,997	3	25	.14
Mussels	15	546	1	14	2,332	1	17	.23
Menhaden	16	450	1	3	18,806	8	31	.024
Butterfish	17	424	3	20	754	–	11	.56
Winter Flounder	18	387		16	1,251	–	16	.31
Cusk	19	290		15	1,594	1	21	.18
Yellowtail	20	220		21	643	–	15	.34
Crabs, Rock	21	213		17	1,253	1	20	.17
Alewives	22	149		13	2,561	1	29	.058
Shrimp	23	126		27	153	–	10	.82
Halibut	24	109		30	69	–	7	1.58
Eels, Common	25	108		29	102	–	9	1.06
Tuna, Bluefin	26	108		31	62	–	6	1.74
Grayfish	27	96		18	1,172	–	27	.082
Mackerel	28	78		23	538	–	24	.14
Skates	29	61		25	390	–	23	.16
Sea Moss	30	61		19	1,010	–	28	.06
Silver Hake	31	60		24	535	–	26	.11
Total	(1-31)	92,472	99.8		242,986	99.5		.381
Total for all Maine Landings		92,674	100.0		244,216	100.0		.379

[a] Calculated from DMR estimates of 172 bloodworms and 82 sandworms per pound (Maine Landings use estimates of 44 bloodworms and 40 sandworms per pound).

[b] All species contributing less than 0.5% to the total landings were left blank.

*Statistics compiled by NMFS and DMR.

examined.

Clams

Gouldsboro Bay has historically been clear of red tide, although shell fish beds are closed by the state when the neighboring bays show signs of contamination. Local people historically have claimed that Gouldsboro clams have never been directly affected by red tide.

Approximately 165 commercial licenses are issued in Gouldsboro township and 125 issued in Steuben. Of the total 290 licenses issued between Gouldsboro and Steuben approximately 130 people will harvest clams on an average of 100 days per season, each producing an average of 1.5 bushels a tide. Most diggers will only work one tide, and therefore 1.5 bushels per person per day is probably a reasonable assessment. One hundred and thirty diggers producing 11/2 bushels amounts to 19,500 bushels harvested from the Gouldsboro Bay each season. At $24.00 per bushel the value of 19,500 bushels is $468,000.00. One bushel will shell approximately two gallons of clam meat, therefore, 19,500 bushels equals 39,000 gallons of shucked meat. Thirty-nine thousand gallons of shucked meat would provide approximately 312,000 pounds of shucked clam meat harvested from Gouldsboro Bay during a season.

Figure 86. Clam diggers working a mud flat at low water.

Figure 87. Herring weir at the northeastern corner of Gouldsboro Bay

Scallops

Scallop beds are sporadically discovered in the Gouldsboro Bay area. Once a bed is discovered it is quickly harvested. According to the Corea co-op, eight boats were rigged for scalloping in the 1980-1981 November - April season. This season was unusual in that 7,000 pounds of scallops were landed from beds a few miles south of Corea. In an average year, i.e., 1981-1982, 2,000-3,000 pounds would be considered a high estimate. Corea co-op records indicate the November - December 1981, 100 - 200 pounds were landed each day. This figure is very low.

One lobsterman reported that in the winter of 1981 a boat from Stonington discovered a scallop bed in Gouldsboro Bay. On the first day, 256 pounds were harvested, the second day 227 pounds, the third day 80 pounds, the fourth 0 pounds. This indicates how quickly the resource is harvested once it is discovered. Very little scalloping apparently occurs in Gouldsboro Bay on a long term basis.

Maine State law limits draggers to four foot drag widths in Gouldsboro Bay. The season is November 1 to April 1, so as not to interfere with lobster traps set during the summer months. According to the State scallop specialist, 30% of the scallop catch in Maine does not go through the dealers; therefore, it is difficult to assess the amount of scallops actually harvested.

Mussels

Although abundant, mussel are rarely harvested in Gouldsboro Bay. Most sizeable mussels that are exposed during low tides are many years old and contain pearls. They are thus not very desirable for the market.

Herring

The Maine Department of Marine resources (DMR) has studied the Maine herring fisheries in great detail, including the biology of the species, catch and landing statistics and the industry's impact on Maine's economy. To clarify terms: catch refers to actual amounts of herring caught in Maine waters; landings are catches plus additional herring caught in Canadian waters or another state that are brought into Maine by boat and landed at Maine ports. DMR records indicate 51,976 metric tons of herring were landed at Maine ports in 1981. Of this total amount, 24,795 metric tons were landed in Maine's eastern section including Gouldsboro Bay.

Three gear types are used to catch herring: purse seines, stop seines and weirs. Gouldsboro Bay has three weirs, Dyers Bay has six weirs and Milbridge has three weirs in Sands Cove. Stop seining is often used in Dyers Bay and Milbridge, but rarely in Gouldsboro Bay. Past records have indicated smaller quantities of herring have been caught in Gouldsboro Bay in comparison to neighboring areas.

Mr. Calvin Stinson of Stinson Canncove in Prospect Harbor provided data on quantity of herring his company purchased from Gouldsboro weirs. Stinson's key suppliers are not local; they purchase herring from Canada to ship to Gloucester, Mass. Only a very small portion of their business is local. Local competition lies between the L. Ray Packing Company and the Jasper Wyman Company, both located in Milbridge. An Interview with Gary Ray of L. Ray canning made it very clear they were not willing to discuss specific landing data. Due to a reduction in the resource and recent federal labor laws affecting overhead costs and operations, a number of canneries in operation for many years have bee forced to close.

Herring season is usually from May through October with the best fishing during the summer months, The herring purchased by Stinson from Gouldsboro Bay weirs were caught from mid-June through Mid-July during the 1981 season. In 1981, Gouldsboro Bay yielded 332 hogsheads or 651,700 pounds or 295.55 metric tons of herring. This amount is 0.6% of the total 51,976 metric tons landed in Maine and 1% of the 24,795 metric tons landed in Maine's eastern section.

Bloodworms and Sandworms

With the assistance of Mr. Bruce Joule, worm specialist from Maine's Department of Marine Resources, we were able to collect available statistical data on this industry, which makes an

Figure 88. Close up of Herring weir with the “trap” section and the fish deflector extending to shore (upper right).

Figure 89. Lone lobsterman retrieves his pots outside of Bald Rock.

important contribution to Maine's fishing income (see Table 18). Worms are harvested for the recreational sport fishery industry for use as bait. Key markets are on Long Island, New Jersey and California, during the summer months when the demand is high.

The State of Maine requires a Maine worm diggers license. There are no restrictions on where worms may be harvested; therefore, worm diggers travel from Wiscasett to Jonesboro to collect worms depending on the market demand. The dealers provide daily limits and prices per worm, and the availability, accessibility and location of the resource. Bloodworms are rarely found in Gouldsboro Bay. Occasionally several have been collected from Noyes Cove in early spring. Sandworms are more prominent and are usually found in mussel beds rather than on clam flats.

Depending on the market and dealers limit, an average count allows 1500 worms collected per person per day. There are two large dealers located in Jonesboro and Hancock. Since travel costs to these dealers would be deducted from the value of one's daily catch, one often see families or large groups often work together to make a trip worthwhile. The value of sandworms averages \$.03 to \$.05 per worm, bloodworms are \$.08 to \$.10 per worm. There are 43 dealers presently listed in the State of Maine. Diggers distribute worms into lots of 125 or 250 before selling them to the dealer.

According to statistics supplied by the DMR, an average of

3,000 sandworms, and an average of 2,000 bloodworms were harvested per person in 1980. According to estimates by local wardens, approximately 100 local residents and visitors traveling between Wiscasset and Jonesboro and harvest from the Gouldsboro area during the summer months. If we assume an average of 3,000 sandworms were harvested per person during the peak season, then approximately 300,000 sandworms were harvested from the bay area. Thus, sandworms harvested from Gouldsboro Bay would contribute $12,000 annually to Maine's worming industry or 1.2% to the total value of the industry. According to DMR estimates there are 82 sandworms per pound. Therefore, 300,000 sandworms equal approximately 3,700 pounds of sandworms landed in 1980 on Gouldsboro Bay.

Lobsters

Jim Thomas of the DMR in Boothbay Harbor provided State statistical landings of lobster. Gouldsboro Bay was included in data collected from Corea to Eastport where 2,100,000 million pounds were landed. There is no breakdown specific for Gouldsboro Bay, although 182 lobster licenses were issued by the state to lobstermen on Corea and Gouldsboro.

The Corea co-op has 47 members, 20 full time fishermen, two offshore in the winter months. Newman Young, manager of the Corea co-op, stated that in the 1981 fiscal year (July 1, 1980 through June 30, 1981), an average of 250,000 pounds of lobsters were landed at the co-op. Each fisherman has 200 - 600 traps. These men do not fish in Gouldsboro Bay; their traps are set south of Corea in inshore waters. The bait used in lobstering is herring cuts supplied by the local herring processors, alewife available in the spring, and redfish trucked in from Frank O'Hara's, Inc., in Rockland, Maine. Several men also used experimental bait prepared by the University of Maine Sea Grant.

Approximately 25 Gouldsboro residents own boats and lobster fish in the bay from July to November. Another 25 Steuben residents moor their boats in Dyers Bay. Local fishermen varied in the number of traps each owned, varying from 80 traps to 300 traps. The majority of these fishermen work part-time and supplement their incomes from clamming, worming or tree cutting and "wreathing" during the Christmas season.

Interviewing three dealers and lobster pound owners indicated that approximately 100,000 pounds of lobsters were harvested from the Bay ten years ago. There has been a steady decline in pounds landed due to 1) fewer men fishing full time and 2) a reduction in the resource.

Many of these same lobstermen that fished actively full time ten years ago are now fishing part time as they approach retirement. Most young fishermen now fish out of Corea or in Dyers Bay. Each dealer interviewed estimated a range of 25,000 to 50,000 pounds presently harvested from Gouldsboro Bay. These dealers were reluctant to discuss their individual landings. The assessment of landing data for Gouldsboro Bay for lobster is somewhat speculative.

Two approaches were used to collect the data:

1) Visual - a daily count of the number of men, boats, days fishes and traps set. This was carried out in an informal way during the summer of 1981.
2) Economic analysis - estimate the annual average income of the fishermen, market value of the product and number of men fishing and estimate the number of pounds landed.

The Department of Maine resources has stated that 21,981,000 pounds of lobsters were landed at Maine ports in 1981, a value of $41,705,000 to Maine's economy. This figure indicates that the value of the lobster fisheries comprises 45% of the entire fishing industry in Maine.

DMR estimates the number of hauls per trap, of all traps set in 1981, totals 33,959,356 hauls. This information provides the calculation that approximately 0.6 pounds of lobster per haul per trap were taken. This figure is close to our estimate made in Gouldsboro Bay during the 1981 summer. Calculations indicated that 0.5 pounds per trap per day was an average yield based on 25 fishermen fishing 5,000 pots annually. The following example demonstrates particular economic input from Gouldsboro Bay lobstermen according to information based on interviews and DMR reports.

Using 50,000 pounds of lobsters harvested per season from Gouldsboro Bay, 25 fishermen, three hauls per week on 5,000 traps and a 16 week season, the following can be calculated: a harvest rate of 0.21 pounds traps haul and a yearly income of $3,840 for 50 days labor. These figures appear to agree roughly with individual lobstermen analysis of their harvest income rate in Gouldsboro Bay today.

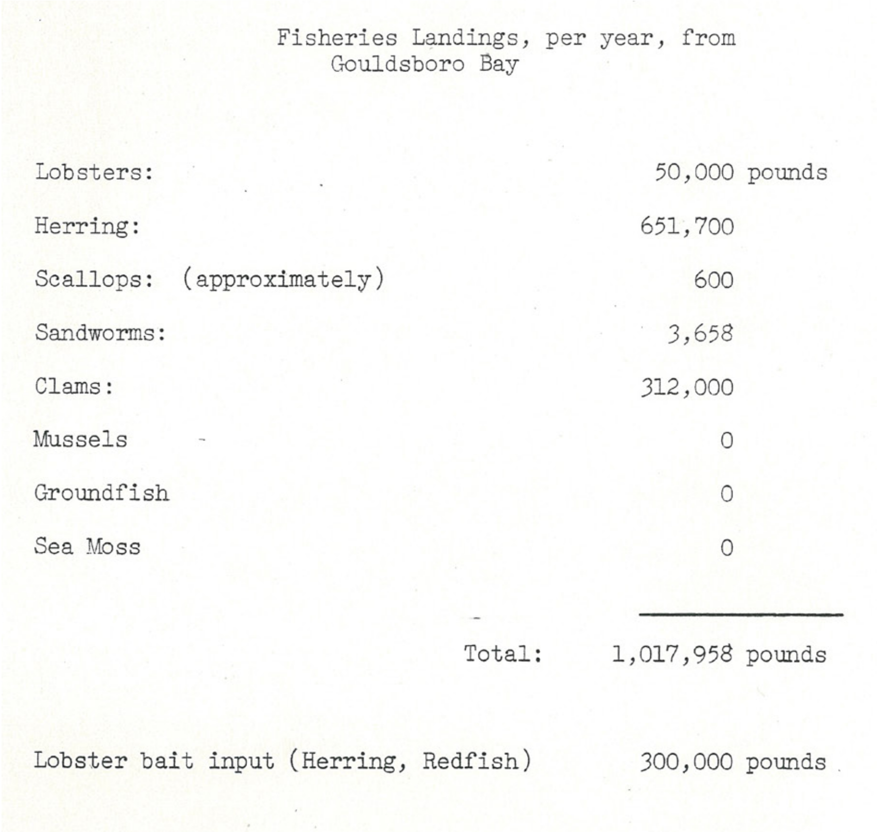
These data, as discussed above, are summarized in table 15.

PRELIMINARY SYSTEMS ANALYSIS

At this point an ecological system analysis of Gouldsboro Bay can only be tentative. Nevertheless, a first attempt is made graphically in figure 90. An effort has been made in the diagram to differentiate between hard numbers (5.8), educated guesses (est. 8) and guesses based on little information (block or arrow without a number). No attempt has been made at this preliminary stage to explain in detail the background of the information.

Most striking about this analysis, as compared to previous generalized treatments for the Maine Coast (e.g. Fish and Wildlife Service, 1980), is the prominent role accorded to primary production by benthic algae (as compared to phytoplankton), and the extensive replacement role of fine macroalgal detritus for phytoplankton. A beach drift stage is

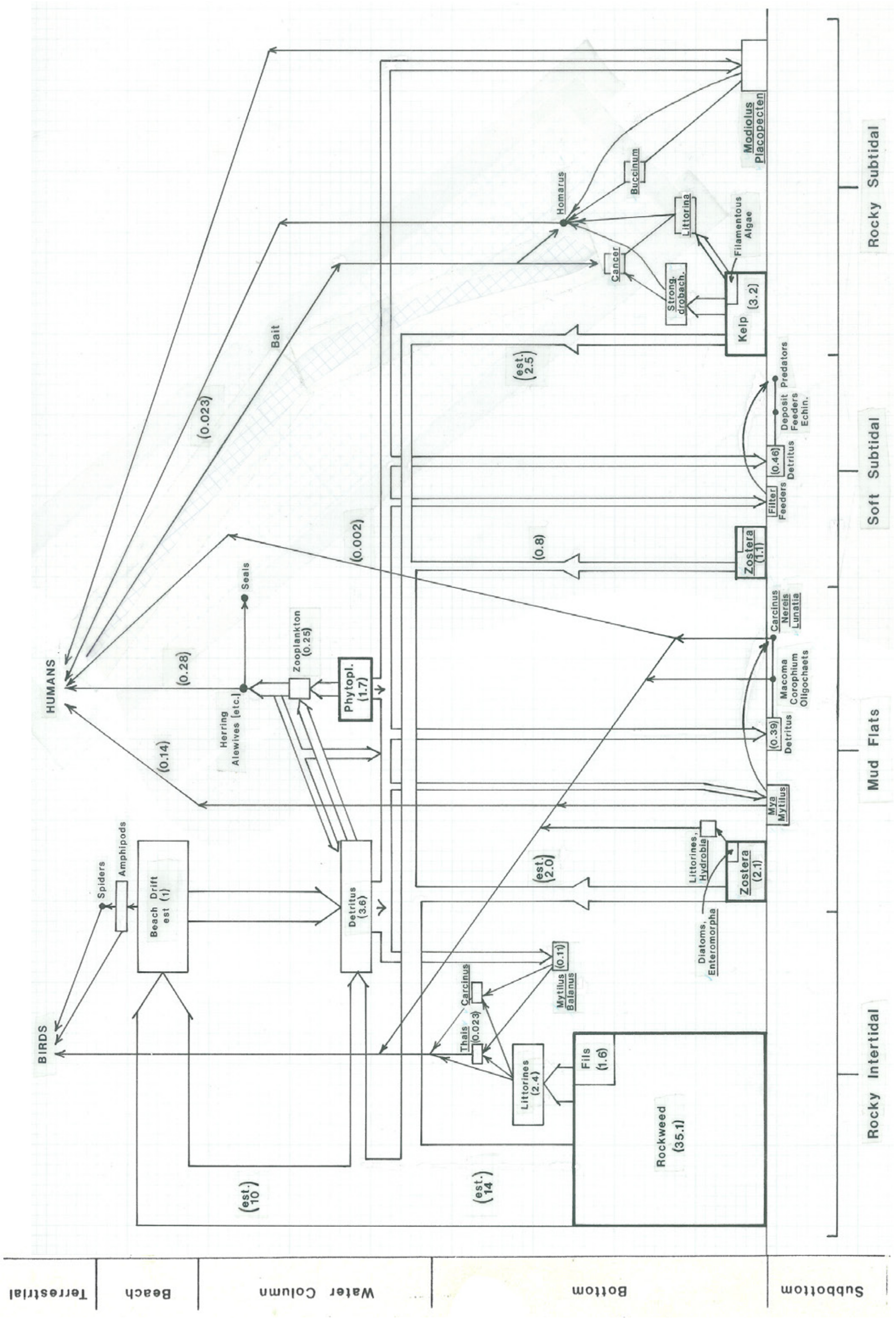
Table 19. Fishery landings per year from Gouldsboro Bay.



Fisheries Landings, per year, from
Gouldsboro Bay

Lobsters:	50,000 pounds
Herring:	651,700
Scallops: (approximately)	600
Sandworms:	3,658
Clams:	312,000
Mussels	0
Groundfish	0
Sea Moss	0
Total:	1,017,958 pounds
Lobster bait input (Herring, Redfish)	300,000 pounds

Figure 90. Preliminary systems diagram for Gouldsboro Bay.



central to the functioning of this detritus system, and a large part of the primary production is cycled through drift (Figures 91-93). Also, quite apparent in this analysis is the very heavy utilization of the bay's biological resources by humans. The equivalent of over 60% of the bays' total primary productivity, as estimated by level in the food chain and the x 10 rule of thumb, is removed by fisheries. An estimate of the total zonal primary productivity is given for bay, inshore and offshore Environments in figure 94.

Figure 91. Determining quantities of algal beach drift on the Western shore of Gouldsboro Bay.

Figure 92. “Algal soup,” breakdown of Ascophyllum on beach.

Figure 93. “Washout” of algal soup at spring tides (Winter Harbor).

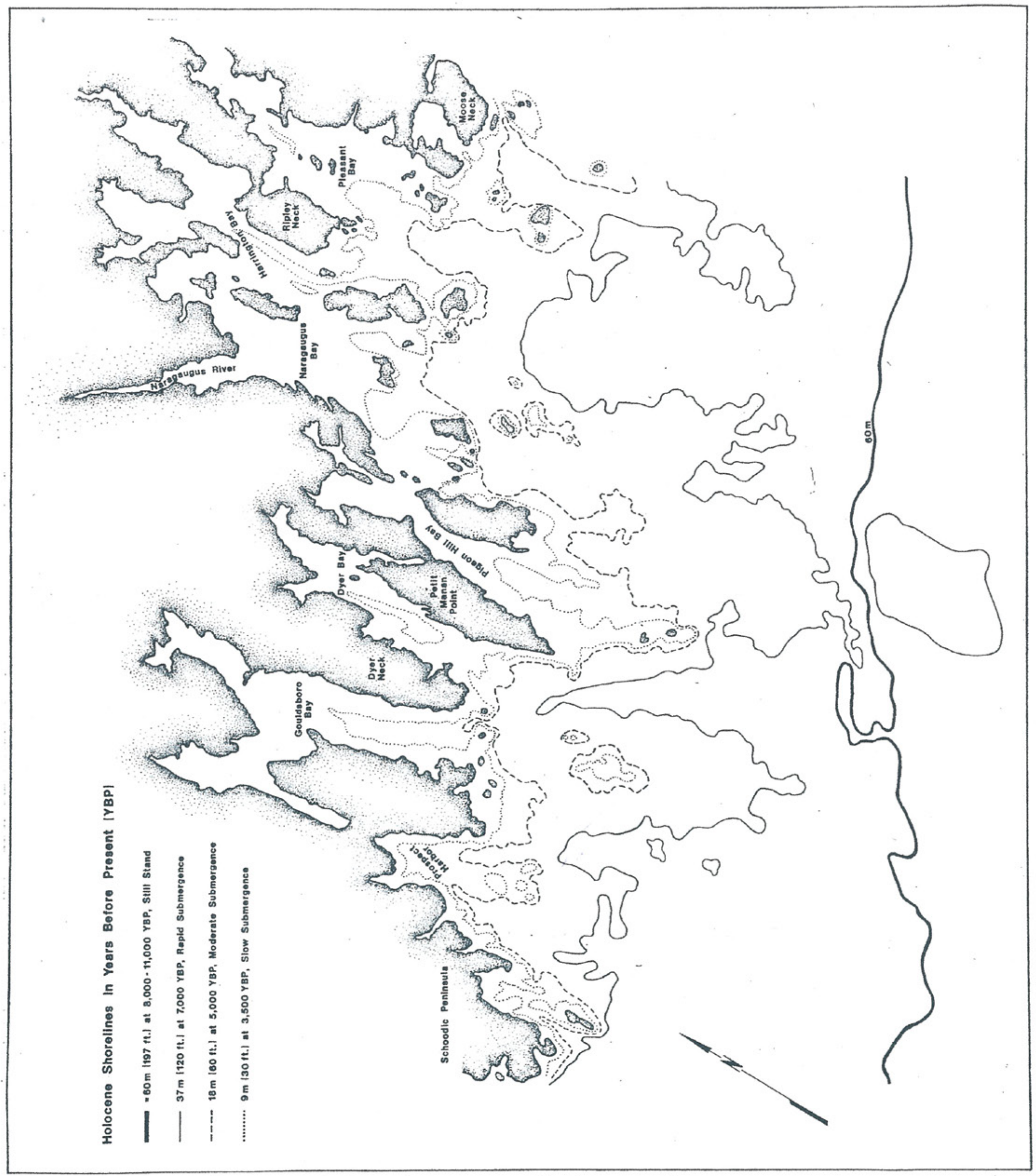


Figure 94. Primary productivity of the bay, inshore and offshore environments of Gouldsboro Bay area.

ACKNOWLEDGEMENTS

A Marine Systems Laboratory (MSL) team of 15-20 scientists, students and supporting staff, as well as participating colleagues from several universities, worked diligently together to produce this study of Gouldsboro Bay. Here I will give specific credit to those individuals that spearheaded the key elements of the investigation, many of whom were simultaneously working on masters or PhD dissertations at participating universities.

Craig Shipp and Stephanie Staples carried out the broad range of geomorphological studies, at times bringing in staff and students from the Geology Department at the University of Maine to assist in the coring and seismic studies. Professor Robert Steneck, based at the University of Maine's Darling Center worked with Michael Brittsen and Jill Johnson to carry out the long term studies of kelp and rockweed production on rocky bottoms. Teena Michael, with assistance from several project staff, analyzed the standing crop and productivity of the narrow band of eel-grass that stretched around most of Gouldsboro Bay. David Packer, with help from virtually all project staff in the tedious screening separation process, examined the ubiquitous soft bottom invertebrate in-fauna, while Silvanna Campello similarly engaged the diversity and productivity of the planktonic community. Although presented elsewhere, and not discussed in this Report, Danielle Lucid worked tirelessly to demonstrate the potential for mussel aquaculture in Maine Bays.

Finally, two key supporting staff who mostly remained back at the offices of MSL in the Smithsonian's National Museum of Natural History, Janice Byrum at the front desk and Charlotte Johnson at the drafting table, made the field work and the preparation of this report possible.

Nancy Foster, at NOAA's Marine Sanctuary Program, had the foresight to see the potential importance of an inshore marine sanctuary in the Gulf of Maine. She and her office provided the funding, as Grant No. NA81AA-D-CZ076 from the Office of Coastal Zone Management, that allowed this project to be carried out.

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