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Ecological Effects of Major Storms on Coastal Watersheds and Coastal Waters: Hurricane Bob on Cape Cod

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ABSTRACT

VALIELA, I.; PECKOL, P.; D'AVANZO, C.; KREMER, J.; HERSH, D.; FOREMAN, K.; LAJTHA, K.; SEELY, B.; GEYER, W.R.; ISAJI, T., and CRAWFORD, R., 1998. Ecological effects of major storms on coastal watersheds and coastal waters: Hurricane Bob on Cape Cod. *Journal of Coastal Research,* 14(1), 218–238. Royal Palm Beach (Florida), ISSN 0749-0208.

Hurricane Bob, a category 3 storm, made landfall on Cape Cod in August 1991, and its effects on watersheds and adjoining estuaries were detected in the ongoing studies being caried out as part of the Waquoit Bay Land Margin Ecosystems Research project. On land, Bob had only minor overall effects on forests; localized wind bursts did snap and break trees in small and widely scattered forest parcels. Wind stripped up to half the leaves of deciduous trees and many herbaceous plants on the watershed, and most remaining leaves were damaged by salt, so that by the end of Aug, Cape Cod forests were defoliated. Damaged growing tips of exposed trees were evident for several growing seasons. The salt exposure was followed by a burst of growth and bloom in some plants during Sep–Oct. Forest invertebrates were disturbed by the storm. Nests of hornets and wasps, for example, were apparently destroyed and the survivors became a serious pest problem: hospital records show a ten-fold increase in cases of wasp stings just after Bob. Populations of these insects did not return to earlier abundance for several years. Birds and mammals did not appear to have suffered much damage. Leaching of salt to soils released previously-adsorbed soil ammonium. Such loss of critical nitrogen may be in part responsible for the characteristically dwarfed near-shore coastal forests, as well as adds nitrogen to groundwater that in turn transports the nitrogen to receiving waters.

On the Bay, Bob thoroughly mixed the water column, but the stratification was restored within 1–2 days after passage of the storm. Short recovery times might be characteristic of shallow bays with short (2–3 d) water residence times. Bob opened a new inlet to Waquoit Bay, which remains open. The new inlet exerts only minor effects on circulation within the Bay, but did create localized damage to dune and eelgrass habitats near the new inlet. The mixing of the water column released major amounts of nutrients that were held within the macroalgal canopy and upper sediments, into the upper layers, and prompted a short-lived (2–3 d) phytoplankton bloom. Biomass of unattached macroalgae was not affected by Bob. Respiration and nitrogen content of the dominant macroalgal species were elevated after passage of the storm, but returned to normal rates after several days. Nearly all above-sediment eelgrass biomass was removed, but returned to previous biomass during the next growing season. There was no visible damage to fringing salt marsh habitats. Damage to aquatic animals appears to have been minimal. A small decrease in water temperature and increased respiration by macroalgae led to decreased total net ecosystem production and increased net ecosystem respiration, but the decreases disappeared after 2 d.

The effects of Hurricane Bob seemed more intense and protracted on land than on aquatic ecosystems. Recovery from the various distubances took hours to days in the aquatic system, but months to decades in terrestrial components. Rigid, larger organisms attached or rooted to substrates seem most subject to storm-related disturbances.

ADDITIONAL INDEX WORDS: *Waquoit Bay, Land Margin Ecosystems Research, hurricanes, storm effects, recovery from disturbance, coastal forests, estuaries.*

INTRODUCTION

In this paper we report results obtained before, during, and after passage of Hurricane Bob over Waquoit Bay, on Cape Cod, Massachussetts. At the time Bob arrived, we had been carrying out long-term studies of terrestrial and aquatic coastal environments of Waquoit Bay on Cape Cod, under the Waquoit Bay Land Margin Ecosystems Research project (WBLMER) (VALIELA *et al.*, 1992; LMER COORDINATING COMMITTEE, 1992). The focus of WBLMER is the coupling and functioning of adjoining land and water systems. The

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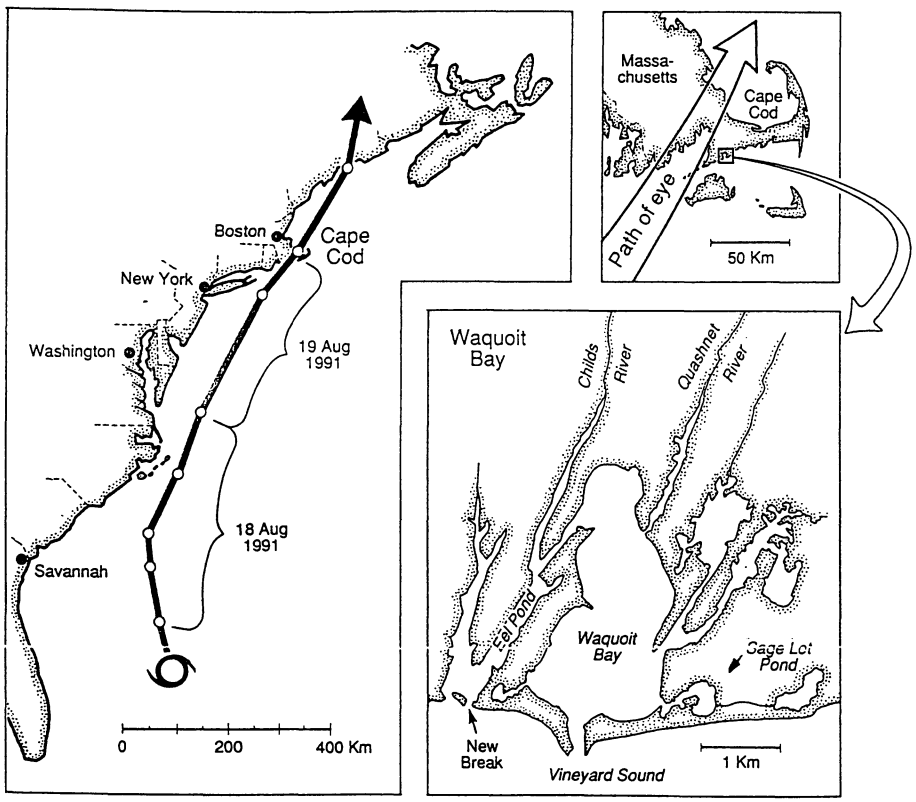

Figure 1. Path of Hurricane Bob along the East coast of the United States. Inset on top right shows the path of the eye of the hurricane over the Cape Cod area, inset on bottom right shows Waquoit Bay and its estuaries.

landfall of Hurricane Bob on Cape Cod therefore gave us the opportunity to assess consequences of a large storm on key processes in coupled terrestrial and aquatic systems, and follow recovery from the effects of the storm.

Hurricanes and typhoons leave their mark on land and aquatic environments through a variety of catastrophic effects. Reviews show long lists of impressive direct effects of major storms on specific components of coastal land and seascapes (DAVIS and LAIRD, 1976; WOODLEY *et al.*, 1981; FINKL, 1994; WALKER *et al.*, 1991; FOSTER and BOOSE, 1992). It is difficult to generalize about effects, however, because hurricanes, typhoons, and tropical storms vary remarkably in wind speed, amount of associated rainfall, time of year, geography of landfall, and hydrographic features such as storm surges. Reported environmental effects are capriciously varied, and may depend on the specific type of ecological system affected by the storms. It may matter if the affected system includes different types of land and aquatic components, such as tropical versus temperate forests, or temperate macrophyte-dominated coastal waters versus coral reefs. Moreover, most studies do not follow up on reports of initial damage, so that recovery is not well-known. The data provided by WBLMER furnish a comprehensive view of effects on adjoining units of land and sea, and of recovery of the different components over periods of days to years, in a temperate shallow coastal system in which coastal temperate forests are the natural vegetation on the watershed, and the aquatic components are macrophyte-dominated.

The information presented in this paper are the result of many different kinds of observations, and include data segments taken from many different types of data collected by the authors. Because the methods are so varied, and because descriptions of the methodology and full data series are available elsewhere, or will be published in separate papers, we mention methods only briefly below, as we discuss the various sets of data, or in the legends to tables and figures. In the next section we therefore present combined results and methods to first introduce some relevant properties of Hurricane Bob, then describe the effects of the storm on the land part of the system, and on the estuarine part of the Waquoit Bay system.

CHARACTERISTICS OF HURRICANE BOB

On 19 August 1991 Hurricane Bob made its landfall on the south shore of Cape Cod after following a path northward from the Bahamas and offshore from the east Coast of the U.S. (Figure 1). The storm arrived onshore at about mid-tide, buffeted Cape Cod for 3 hr, and quickly pressed northward. Bob was a category 3 storm (BRENNAN, 1991, and Table 1) as it made landfall, with wind gusts reaching up to 160 km per hour. A storm surge 2–4 m above mean tide levels was

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Table 1. *Numbers of plants of the sand plain gerardia (*Agalinus acuta *Pennell) in two sites in Cape Cod, over several years before and after Hurricane Bob. Data provided by P. Somers, National Heritage and Endangered Species Program, Massachussetts Division of Fish and Wildlife.*

Year	Nearshore Site	Inland Site
1987	18	—
1989	330	—
1990	1362	1702
1991[a]	0[b]	150[b]
1992	42	—
1993	349	—
1994	798	—

[a] Counts taken after passage of Hurricane Bob
[b] All plants killed by salt spray from Hurricane Bob

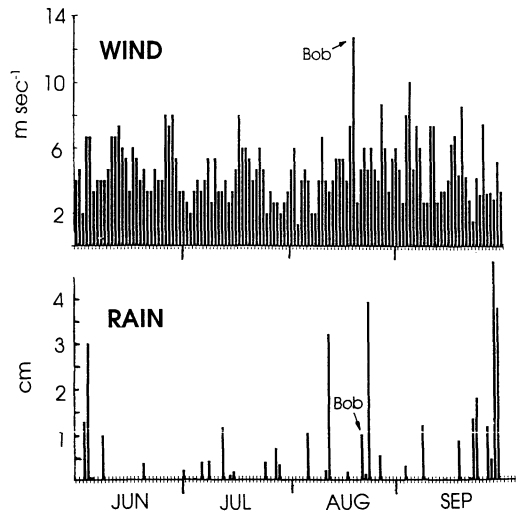

Figure 2. Records of average daily wind velocity (top) and rain (bottom) during summer 1991. Data from Otis Air Force Base Meteorological Station, Cape Cod, Mass.

associated with passage of the eye of the hurricane. The average wind velocity during 19 Aug 91 was 3 times higher than usual for the Jul–Aug period (Figure 2 top), even though Bob only spent 3 h passing over Cape Cod. Rainfall reached up to 20 cm in some places along the path of the storm south of Cape Cod. Bob was a reasonably dry storm in the Cape Cod area, but was followed by two days of additional rain (Figure 2 bottom).

Winds were the principal agent of damage on land, which was widespread (Figure 3). Power and telephone lines were down up to a week after the storm; repair crews from as far as Buffalo, New York, and Baltimore Md., worked around the clock for one week to restore electricity and communications (Figure 3 top left). Most roads were impassable because of the tangle of downed trees, utility poles, and wires, or because of undermining or flooding. Innumerable boats were beached (Figure 4 left panels), damaged, or sunk. The north shore of Waquoit Bay and elsewhere on Cape Cod were littered with boats, boat fragments, broken glass, and flotsam. Buildings near beaches suffered considerable damage (Figure 4 top right). Wind and water motion were powerful enough to drive bits of vegetation into shingled walls of buildings near shore (Figure 4 bottom right). Casualties were fortunately low, with few hurricane-related deaths.

The ongoing WBLMER work provided data one cological components and processes before and after passage of the hurricane. With these data we document direct and indirect effects of the storm on land and sea, and examine course and duration of recovery of various components.

EFFECTS ON LAND

Direct Effects

First-order effects of Hurricane Bob on forested coastal areas included blowdowns and trunk snapping, limb breakage, defoliation of trees, and killing of herbaceous vegetation.

Only a small proportion (< 3%) of trees were blown down or snapped by winds over most of the dominant oak-pine forests surrounding Waquoit Bay. Most hurricanes cause relatively modest tree mortality, ranging up to about 40% of stands (Figure 5).

As in the case of Hugo in Puerto Rico and in South Carolina (HOOK *et al.,* 1991), and Andrew in Florida (LOOPE *et al.,* 1994), most of the trees that were blown down during Hurricane Bob in the Waquoit Bay area were taller, older individuals. In Cape Cod, these larger trees evidently had survived for decades because Cape Cod had not been subject to a hurricane comparable to Bob since 1955. Many of the larger trees that were blown down had hollow trunks.

Damage to trees depended on the species, as found in studies of other hurricanes (HOOK *et al.*, 1991; FOSTER and BOOSE, 1992; LOOPE *et al.,* 1994). In Cape Cod, stands of white cedars, or black locust growing on wetter soils, were more severely (although locally) affected by blowdowns than oak-pine forests. The frequency of blowdowns of individual trees partly depends on where they grow. Blowdown frequency varies with exposure and wind direction (FOSTER and BOOSE, 1992). Exposure to wind was greater in edges along roads, forest edges, and in residential tracts, where many large maples, pines, oaks, elms, and ashes were blown over (Figure 3 top right). Tree species with shallow root systems (for example, white cedars on Cape Cod, mangroves in Florida) are the most susceptible to toppling during severe storms. In the wake of Hurricane Andrew, up to 95% of red mangrove trees were uprooted (or snapped) in certain mangrove fringes of southern Florida (SMITH *et al.,* 1994).

Blowdown damage may also depend on amount of rainfall associated with the storm. Damage to Cape Cod forests by wind was less than what could be expected because of relatively light rainfall during the hurricane (Figure 2 bottom). Most of Cape Cod was on the east side of Hurricane Bob; the eye travelled over Buzzards Bay and the Cape Cod Canal (Figure 1 inset). Waquoit Bay and its watershed were therefore on the drier quadrant of the storm, and so, during the most intense period of winds, soils were not sodden with moisture, and tree boles were not laden with water. Both these circumstances reduced blowdowns in Cape Cod, but we should be slow to generalize, since Hurricane Andrew was also a fairly dry storm (PIMM *et al.*, 1994), yet, probably be-

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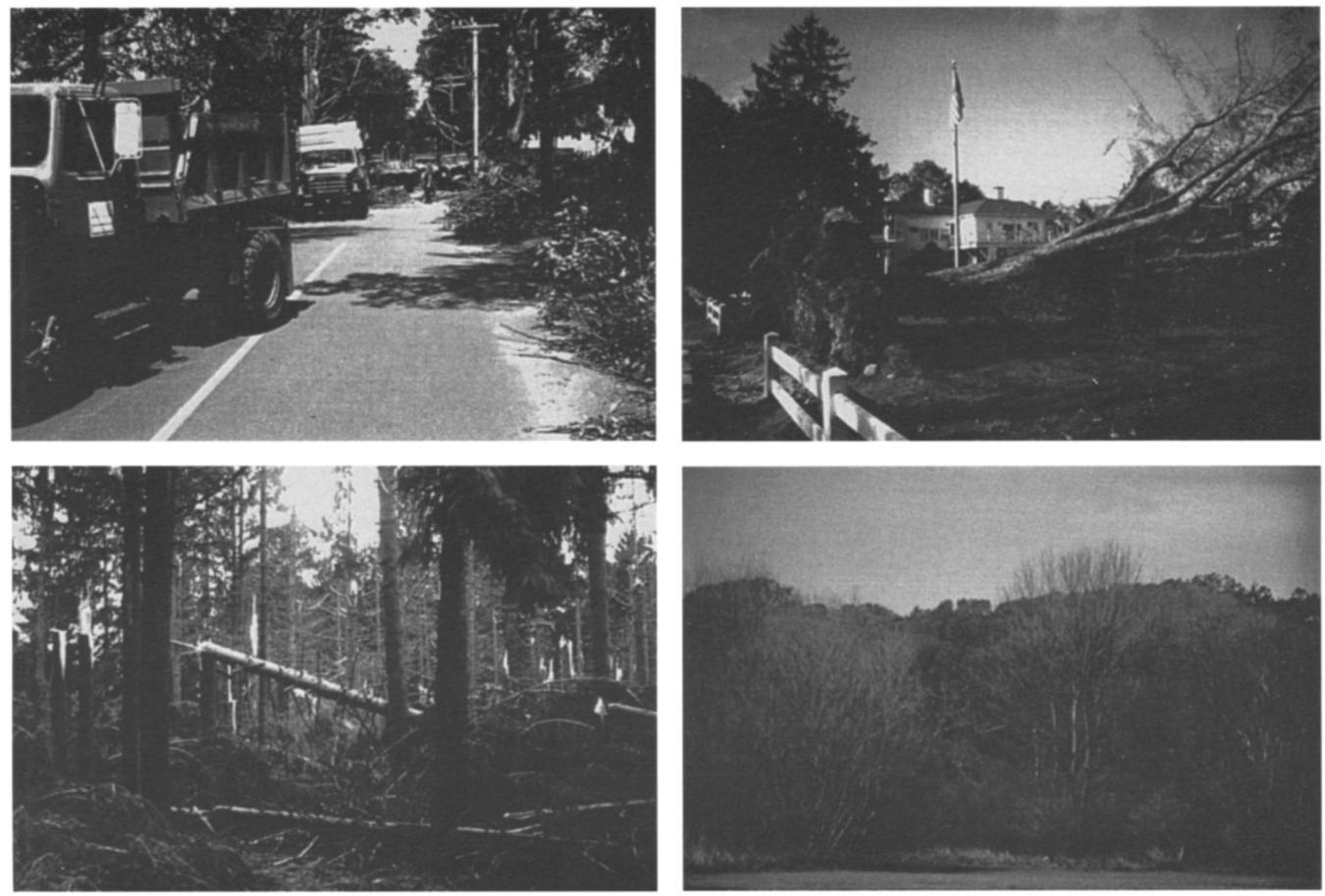

Figure 3. The aftermath of passage of Hurricane Bob in Falmouth, Cape Cod: Some effects on terrestrial environments. Top left: Work crews clearing storm-blown trees from streets within a few days after the storm. Top right: Blowdowns of large trees were common in exposed sites such as residential areas or forest edges. Bottom left: Spruce plantation where high-intensity local bursts of wind broke most of the trees. Bottom right: Dead vegetation in wet woodland near shore; this area had been flooded by seawater for a few days after the storm. Green trees behind were on higher ground, and were not flooded. Photographed during summer of 1992.

cause of stronger winds (Figure 3) and magnitude, it produced significant tree mortality by blowdowns and trunk snapping.

Breakage of limbs or trunks in Cape Cod forests during passage of Hurricane Bob was more common than blowdowns, as found in nearly all cases, for instance in South Carolina forests affected by Hugo (HOOK *et al.,* 1991). In the Cape Cod area, a third to half of the trees on most forest stands near shore sustained some limb breakage. The trees most severely affected by limb or trunk breakage were spruces and black locusts. Trunk and limb breakage was spatially non-uniform, as found elsewhere (FOSTER and BOOSE, 1992). The spatial heterogeneity is probably the footprint left where a complex of small tornado-like eddies, referred to as "wind microbursts" by POWELL and HOUSTON (1993), reached the ground. In the case of Hurricane Bob there were scattered parcels within spruce stands where most trees up to 40 cm diameter breast height were broken off at about 1–3 m (Figure 3 bottom left). The physical appearance of these parcels one growing season after the storm, with dense undergrowth and ragged standing trunk remnants, were reminiscent of damage caused by Hurricane Hugo to forests of Puerto Rico (WALKER, 1991; BROKAW and GREAR, 1991) and South Carolina (HOOK *et al.,* 1991). A similar pattern of localized trunk snapping was also recorded in Florida pine forests after Andrew (LOOPE *et al.*, 1994).

Leaf removal and damage was another first-order effect of Hurricane Bob. The wind stripped from a third to half the leaves off deciduous trees, and many of the remaining leaves were bruised (*personal observation*). Evergreen leaves were less affected by the wind, as also reported in Florida (LOOPE *et al.,* 1994).

Blowdowns and trunk snapping are more likely to lead to tree mortality than defoliation. In general, however, tree mortality is surprisingly low in most hurricanes, and is, as might be expected, proportional to wind velocity (Figure 5). Hurricane Bob was at the low end of both wind velocities and tree mortality and severe damage. Even in the most intense storms studied, however, less than 40% of trees were killed or severely damaged (Figure 5).

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Figure 4. Aftermath of Hurricane Bob: Effects on shore. Photos taken the day after the storm. Wind and water were moving fast enough to wedge straws into shingles in buildings flooded by sea water.

The herbaceous layer was also damaged by salt spray. Records of abundance of sand plain gerardia (*Agalinus acuta*), an endangered herbaceous species, serve as a proxy to assess impact of the storm on herbaceous vegetation on land. There are two populations of this rare species in Cape Cod, one in a site near the shore, a second farther inland (Table 1). These populations had increased markedly between 1987 and 1990. In both sites there was a drastic reduction in plant stem counts after passage of Hurricane Bob (Table 1). Reestablishment from seed banks in soil have allowed recovery of the

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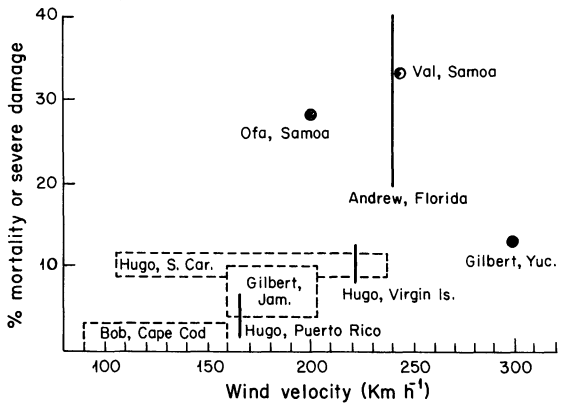

Figure 5. Relationship of the % of trees that were dead or severely damaged, and wind velocity for various hurricanes. Data from present study and BELLINGHAM *et al.* (1992), FANGI and LUGO (1991), WHIGHAM *et al.* (1991), LOOPE *et al.* (1994).

species since 1991. Sand plain gerardia, and probably most of the herbaceous species in our area, seemed to recover from hurricane damage within a few growing seasons. In our case, the mortality came from salt exposure, but fires are common in our pine oak forests, and the life cycle of gerardia may be adjusted to such disturbances.

Indirect Effects

Higher-order effects of Hurricane Bob on land plants, animals, and soils included off-season leaf drop, leaf regrowth and flowering, disturbances to animal populations, and leaching of soil nitrogen.

Off-Season Leaf Drop

In addition to being bruised by the wind, leaves that remained on trees were dehydrated, and probably more importantly, covered by wind-borne salt spray. Within a few days after Bob nearly all deciduous leaves still on stems died. At the end of August the appearance of forests in Cape Cod was comparable to what would be expected in late November-early December (Figure 6 top left). Trees whose complement of leaves were dead and brown were evident within a coastal strip of up to 7 km from shore [notice the brown color (seen as a lighter shade) of the vegetation in the aerial view of Figure 15 top, taken in 1991, compared to the green (darker) appearance of vegetation in the other photos of Figure 15]. Some trees with dead leaves could be seen even farther inland. Such delayed defoliation appeared also in mangrove trees after Hurricane Andrew in Florida (SMITH *et al.*, 1994). In the case of mangroves, dehydration by wind seems more likely as the responsible mechanism, since these are halophytic species supposedly well suited to exposure to salt.

Leaf death occurred in Cape Cod forests even though there was a 6–9 cm downpour 2 d after Bob (Figure 2 bottom). The rain rinsed most of the salt off trees and into soils, but the rinsing did not prevent leaf death. The leaf damage created a sudden and early leaf fall, which must have been richer in nutrients, since there was little opportunity for translocation. This new litter appears to have degraded quickly, because by the end of October we could not measure significant increases in litter in affected sites (unpublished data), unlike reports for mangrove tree litter in Florida after Andrew (SMITH *et al.*, 1994).

Damage to Buds

Salt damage to bud set in trees of Cape Cod forests was evident the year following passage of Bob. It was common during spring and summer of 1992 to find that tender twigs and buds on tips of branches were dead, most prominently on the windward southern side of trees (Figure 6 middle left). This dead tip damage is not found in non-storm years, nor inland. Such a pattern of salt sculpting is common within 100 m or less in all shores but in the case of areas affected by Bob, the damage extended much farther inland (Figure 7). The proportion of deciduous trees subjected to such damage was of course higher near the sea, but even at considerable distances inland, exposed trees showed evidence of storm-related damage (Figure 7).

Regrowth and Early Bloom

Another second-order, and unexpected, effect of Hurricane Bob was a widespread regrowth of new leaves, and blooming, on trees and shrubs that lost their leaves (Figure 6 top middle right). This regrowth occurred 3–6 weeks after the storm, and was presumably from buds that normally were to grow the following spring. The exposure to salt and wind somehow reset the timing of bud growth, and many species of spring-flowering plants bloomed during late September to early October (Figure 6 middle right). Unseasonable blooms were seen in cherry, apples, hostas, lilacs, horticultural and native roses, rhododendrons, horse chestnuts, and other plants. Perhaps as a related consequence, blooming and new leaf growth were sparser than normal during the spring of 1992. In addition, many deciduous trees showed recognizably thinner boles during the 1992 growing season (Figure 6 bottom left), but not in subsequent years.

Damage by Salt Water Flooding

Death of complete stands of vegetation was not an important consequence of Hurricane Bob, because there is little extensive floodable area in the hilly topography of Cape Cod. There were only a few hectares of woodlands where seawater from the storm surge stood over soil for sufficiently prolonged periods (several days) so as to kill vegetation (Figure 3 bottom right). This was unlike the case of the extensive flat floodplain in South Carolina, which was flooded as a result of Hurricane Hugo. Flooding by seawater killed extensive areas of the South Carolina coastal forest (BLOOD *et al.*, 1991). Susceptibility to seawater flooding, and consequent forest damage in coastal landscapes, not surprisingly, depends on near-shore topography, and perhaps duration of flooding.

Disturbances to Terrestrial Animals

Some animal populations were thoroughly disturbed, while others seemed largely unaffected by the passage of Hurricane

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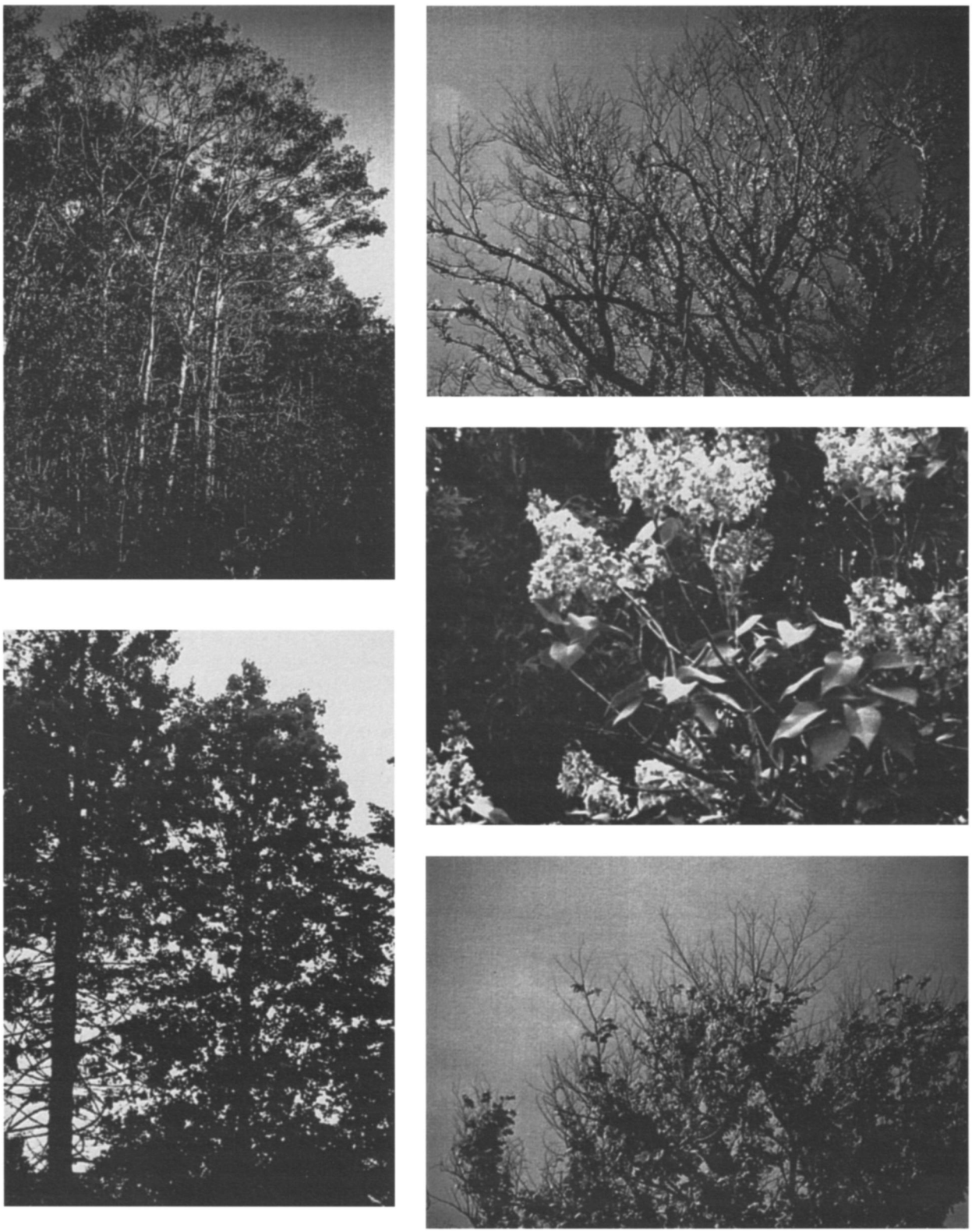

Figure 6. Aftermath of Hurricane Bob. Second-order terrestrial effects. Top left: Premature death of leaves remaining on trees, photo taken at end of August, 1991. Top right: Unseasonable budding of new leaves, end of September, 1991. Middle right: Lilac blooming out of season during September, 1991, after passage of Hurricane Bob (photo by Ron Schloerb). Bottom right: Tree branch tips killed by salt spray from hurricane, spring 1992. Bottom left: Thinner boles commonly seen during summer 1992, nearly a year after passage of Hurricane Bob.

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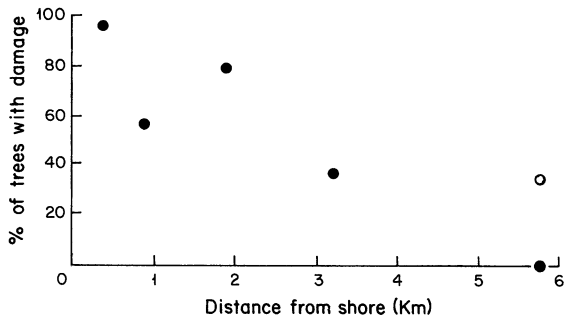

Figure 7. Percent of trees that showed evident signs of leaf and shoot tip damage (as shown in Figure 4 bottom left) in forest tracts located at different distances from the shore. Data from visual counts done along transects approximately 200 m long and 20 m wide. Black points from level ground; white point from a cliff exposed to windward.

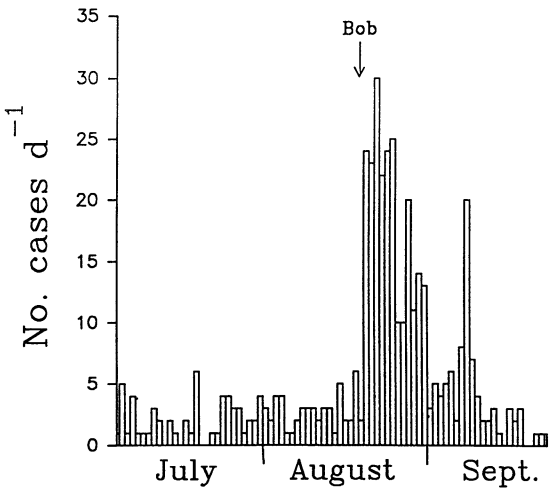

Figure 8. Number of cases of wasp stings treated at Falmouth Hospital, Cape Cod, during the period July–September, 1991. Data courtesy of Roy Hitchings and Susan Douglas of Falmouth Hospital, Falmouth, Mass.

Bob. Forest invertebrates, for example, were drastically affected by habitat damage caused by Bob. A vivid proxy for evidence of profoundly disturbed populations of invertebrates is the record of hornet stings treated in Falmouth Hospital (located in the same area as Waquoit Bay) before and after Bob (Figure 8). Passage of Hurricane Bob was followed by the Cape-wide appearance of remarkably abundant and bothersome wasps. The most abundant species was *Vespula maculifrons*, a yellowjacket that is reported in the literature to nest colonially in the ground, and rarely, in hollows in trees. The bald-faced hornet, *V. maculata*, was less abundant. This latter species builds nests that hang from tree branches. During the remainder of August after Bob, and into early September, it was nearly impossible to have outdoor picnics without attendance of hordes of yellowjackets and hornets. Restaurants closed their open-air serving areas because of the wasps.

Tree limb breakage must have destroyed aerial nests of bald-faced hornets, but is is more difficult to explain the onslaught of yellowjackets, since the storm is unlikely to have harmed underground nests. The disturbance created by Bob may suggest that, contrary to the entomological literature, yellowjackets might nest in tree hollows in Cape Cod, where the loose, unconsolidated soil may not be conducive to construction of underground nests. Hurricane Bob, as mentioned, blew down hollow trees, and hungry, nest-less hornets were apparently forced to uncharacteristically forage for themselves. In addition, for many days after the storm, the defoliation and breakage of tree limbs imparted a heavy, sweet smell to the air, presumably from tree sap. The pervasive sweet aroma seems to have been further disorienting to the nest-less hornets (*personal observation*). The decimation of the hornet populations was evident for several years. In summer of 1994 the hornets in our area were still less common than before Bob, and only by summer 1996 were these insects noticeably common (*personal observation*). The degree of disturbance to land invertebrates suggested by the wasp data suggests that Hurricane Bob is likely to have resulted in reductions in pollination, seed dispersal, herbivory, and other invertebrate-mediated processes in forest communities, and these effects lasted several growing seasons.

Birds survived Hurricane Bob well, judging by two lines of evidence. First, casual observations confirmed continued presence and activity of common summer species such as house and carolina wrens, orioles, mockingbirds, catbirds, titmouses, chickadees, and other songbirds. Second, there were no detectable effects of Hurricane Bob on resident bird species, judging by surveys done in late Dec. (Figure 9). Christmas Bird Counts have been carried out under the sponsorship of the Massachussetts Audubon Society in the Cape Cod area yearly since 1972. The counts are done by expert birders, and cover the same 15 mile-radius parcels. We selected data on abundance of species of birds that reside year-round in

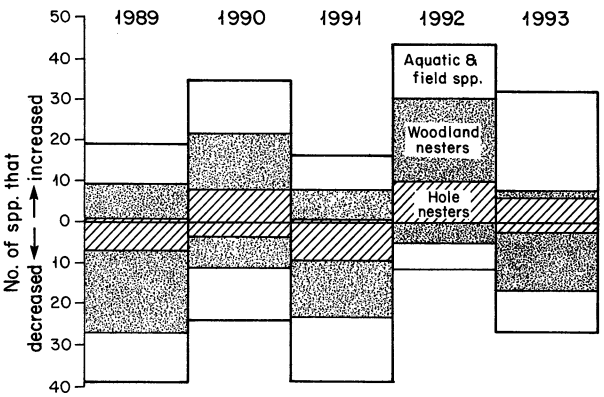

Figure 9. Number of bird species that increased in abundance from year to year (shown as positive changes), and numbers of species that decreased in abundance (shown as negative changes). Data based on Christmas Bird Counts (LeBaron, 1989–1993) for species of birds that are year-round residents of Cape Cod.

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Cape Cod, and thus presumably were exposed to the hurricane. From the CBC records we compiled the number of species that increased in abundance, and the number that decreased in abundance between succesive years. Although more species did decrease during 1991 than in adjacent years, a similar decrease took place in 1989, a storm-less year. The data show that the storm did not unusually affect abundance of resident bird species. To see if different groups of birds were differentially affected, we further subdivided the CBC data into three categories: species associated with water and fields, woodland nesters, and tree-hole nesters (Figure 9). There were no clear effects on any of the three groups of birds, even though we would have expected that species that depend on tree holes might have been most affected by the blowdowns. In the case of Andrew, for example, red-cockaded woodpeckers, which require old, fungus-infested trees, were affected to some extent (LOOPE *et al.,* 1994). In Cape Cod, most land birds had completed fledging their first clutch, and even their second, by the time Bob struck, which might explain in part why the overall effect of tree damage on songbirds was so modest. Abundance of water-associated birds, such as gulls, terns, shorebirds, and waterfowl was also not changed by the hurricane. A Caspian tern, normally a more southern bird, was brought north by the storm, and was seen in Waquoit Bay the day after the storm.

Most hurricanes thus seem, for the most part, to pose modest threats for birds. Much like Bob, Hurricane Andrew also had minor effects on Florida birds (LOOPE *et al.*, 1994). Hurricane Hugo had somewhat more important effects on South Carolina songbirds and waterfowl, by mortality and habitat alteration (MARSH and WILKINSON, 1991; CELY, 1991). The differences cannot be related to the different intensities of the storms; Hugo was a category 4 storm as it made landfall, Andrew was even more intense, with winds speeds of up to 242 km h^{-1} (PIMM *et al.,* 1994). Time of year, types of forest, and other factors may be involved, but in any case damage to birds from Bob seems relatively minor.

Hurricane Bob may have had minor effects on mammals. We found no direct evidence of mortality; a few juvenile grey squirrels were found alive on the ground, apparently thrown from nests in trees that fell or broke. It may be that vertebrate wildlife was tolerant of disturbances prompted by Hurricane Bob, as well as in other storms (CELY, 1991).

Salt-Enhanced Leaching of Ammonium from Soils

Passage of Hurricane Bob also prompted alterations to soil processes near shore. In general, soils closer to shore chronically receive more wind-borne salt than soils further inland. During Hurricane Bob, salt spray travelled further overland than was the norm, and hence inland transport of salt to soils increased. The relative exposure to salt spray is made evident by the difference in range of sodium content of soils before Bob; nearshore, where there was chronic exposure to sea salt spray, soils normally contained 10–15 mg/l, while farther away from shore, sodium concentrations were normally less than 10 mg/l (Figure 10).

The increase in salt delivery to soils released previously adsorbed ammonium (Figure 10 bottom). In spite of the larger concentrations of Na^+ in nearshore soils, there was a greater release of ammonium in inland compared to nearshore soils. Presumably, nearshore soils, exposed to chronic low-level salt inputs, retain only a small amount of adsorbed ammonium on exchange sites. Soils further inland, less ex posed to salt spray, seem to retain a considerably larger pool of adsorbed ammonium. These data suggest that nearshore soils may be depauperate in nitrogen as a result of chronic exposure to salt spray. It may be that the lowered nitrogen supply (in addition to the effects of salt damage to growing tips) might be responsible for the characteristic lowered production and biomass of near-shore forests. In the case of forests in the Waquoit Bay watershed, for example, the canopy of the pine oak forest in the site 0.5 km from shore is only 1–2 m high, in contrast to the canopy in the site 2 km away from shore, which reaches 10–20 m.

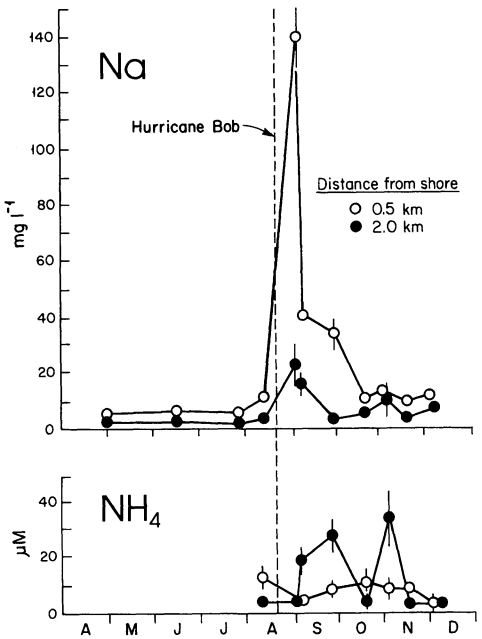

Figure 10. Sodium and ammonium concentrations in water collected in lysimeters located under forest soils at sites situated 0.5 and 2 km from shore, over the period April–December, 1991. Methods as reported in LAJTHA *et al.* (1994).

Under normal circumstances, atmospheric ammonium is retained in forest trees and soil during the growing season (LAJTHA *et al.,* 1994), and may be released during winter, or after large rainfall, such as occurred during August 1992 (Figure 11). Salt delivered by Bob to coastal forests altered the normal pattern, and resulted in a net short-term loss of ammonium from forest soils during the month following passage of the storm (Figure 11). The pulse of salt must have also impaired ammonium retention capacity of the soil-plant ecosystem for some time after the storm, because of sodium saturation of cation exchange sites in the soil, and perhaps the salt could have damaged roots and microbes.

The ammonium released by the salt pulse could be transported seaward by groundwater. The effect of increased re-

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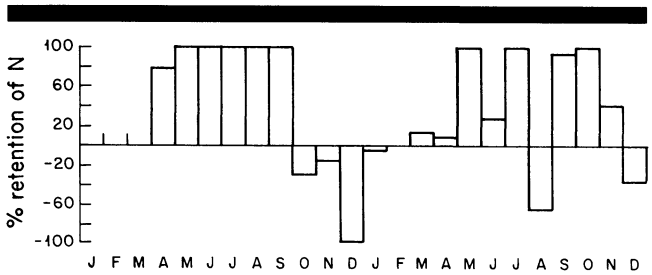

Figure 11. Atmospheric nitrogen inputs retained by forests in the Waquoit Bay watershed, from April to December 1991. Retention of atmospheric nitrogen calculated as in LAJTHA *et al.* (1994), [throughfall nitrogen concentrations − lysimeter nitrogen concentrations] / throughfall nitrogen concentrations. The bars show the retention during the period before the date indicated; this is a section of data from a longer record reported in LAJTHA *et al.* (1991).

lease of nitrogen should be felt at the seashore for some time, since groundwater bearing nitrogen to the sea travels roughly 100 m y^{-1} in the Cape Cod aquifer (LEBLANC, 1984). This means that since Bob delivered sea-salt spray up to 7 km inland, the effect of the 4-fold pulse of ammonium concentration created by the passage of Hurricane Bob below the soil within the watershed will be arriving at the shore over the next 70 years, unless there are losses in the aquifer.

To place the salt-generated nitrogen inputs in perspective, we note that inputs of dissolved inorganic nitrogen (DIN) from forests to Waquoit Bay on average constitute 21% of the total annual inputs to the Bay (VALIELA *et al.,* in press). An increase of 400% DIN release (Figure 10) during one month (Figure 11) adds about 25% to the nitrogen delivered through forests to the Bay. This is a significant increase, but the salt fell on the watershed surface at different distances from shore. The nitrogen released from soils will therefore take different lengths of time to reach the shore, and so the salt-generated increase in ammonium will be delivered to the Bay over perhaps 70 years. Such an increase may therefore have detectable effects only at decadal time scales.

Although other studies have also shown release of soil ammonium after salinization (BLOOD *et al.,* 1991), the results reported here are a first indication that there are important spatial implications. Distance from shore matters in regard to status of the soils, and their ability to support vegetation, and in regard to the coupling between a watershed and its receiving waters. Leaching of nitrogen from coastal forest soils demonstrated by results of the Bob studies show a rare instance of a mechanism whereby the sea affects the watershed. Most other mechanisms that couple land and sea environments involve land affecting the "receiving" waters (*i.e.* VALIELA *et al.,* 1992). Nonetheless, the leaching of soil ammonium to soil water must also act as a positive feedback that increases ammonium transport toward the sea, increasing delivery of watershed-derived nitrogen to the receiving estuary.

EFFECTS ON THE ESTUARINE SYSTEM

Hurricane Bob created a series of direct effects on estuarine ecosystems within Waquoit Bay, prompting changes in hydrography, on barrier bar outlets, on chemistry and biology of the water column, on bottom vegetation, and on animals. The agents of disturbance were the strong S–SE winds (Figure 2 top), and the 2–3 m storm surge associated with passage of the storm. Manifestation of the power of the hurricane was provided by the numerous vessels blown and stranded on beaches (Figure 4), sometimes at surprisingly high elevation above mean low water (Figure 12 top left). The wind and surge were enough to float a 35 foot-long ketch, plus its intact mooring, completely over a barrier spit covered by salt marsh cordgrass; there was no damage to boat, mooring, or marsh grass (Figure 12 bottom).

Hydrographic Effects

Wind associated with the storm completely mixed the water column during passage of Hurricane Bob. The shallow depths of Waquoit Bay and its estuaries makes them particularly susceptible to the effects of wind-forcing (GEYER, 1997). The rate at which wind- and wave-induced turbulence will erode the thermocline can be estimated from a semi-empirical relationship from TURNER (1973, p. 300):

$$T_m = [(\Delta\rho/\rho)gh^2]/15u_*^3,$$

where T_m is the time scale for vertical mixing, $\Delta\rho$ is the density difference between the upper and lower layers of water, g is the acceleration of gravity, u_* is the friction velocity due to the wind stress ($u_* = \tau_w/\rho$), and τ_w is the wind stress. The friction velocity u_* varies approximately linearly with wind speed, so the timescale of mixing decreases rapidly with increasing winds. For the stratification conditions in the Quashnet River, a wind speed of 10 kts would produce a mixing timescale of 1.4 days, while a wind speed of 40 kts would mix the water column in about 10 min. The 1.4 day timescale is longer than the residence time in the estuary (0.4–1 d), which explains why it stays stratified under normal wind conditions. Sustained winds of 20 kts would be adequate to homogenize the estuary more rapidly than it would be restratified by freshwater input. Since winds during Hurricane Bob markedly exceeded 20 kts, wind action during the storm therefore almost certainly mixed the water column *during* the 3 hr passage of Hurricane Bob.

In contrast, only minor hydrographic effects were detectable *following* the storm. Surface waters were slightly freshened during and following Bob (Figure 13); the freshening effect was manifested most clearly during high tides, when the salinity of surface water (normally 31–32‰) failed to exceed 25‰ for 4 d after the hurricane. Surface salinities returned to pre-storm conditions by 26–27 August 1992. We should note, however, that lowered salinities were also recorded on 17 and 27 Aug, so that the freshening that followed Bob was not out of the ordinary.

Bottom waters became somewhat saltier after Bob (Figure 13), but returned to pre-storm conditions after one week or so. After the storm, the water column of Waquoit Bay showed increased vertical stratification, probably as a result of the input of salt water from the storm surge and the increased freshwater from precipitation that followed the storm (Figure 2 bottom).

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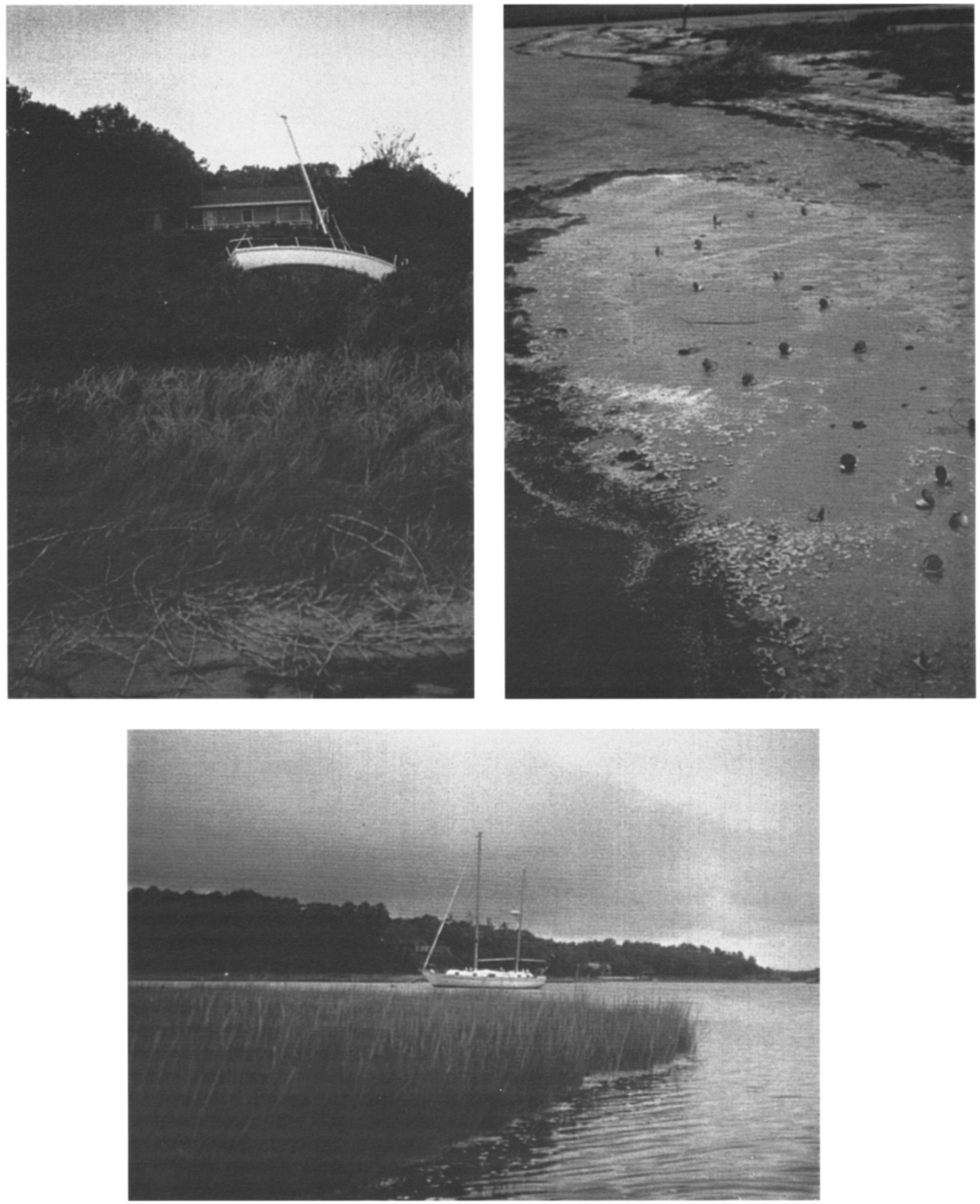

Figure 12. Aftermath of Hurricane Bob: More effects in the shores of Waquoit Bay. Left: Sailboat stranded by post-Bob surge about 5 m above mean tide level. Right: Scallops dead on shore the morning after passage of Bob. Bottom: ketch that was floated by storm surge over marsh-covered bar.

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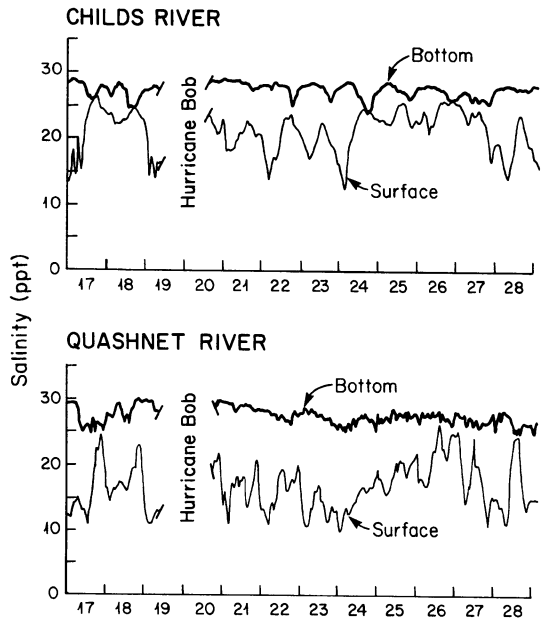

Figure 13. Salinity of surface and near-bottom water in Childs River and Quashnet River, two estuaries of Waquoit Bay, over the period 17–28 August 1991. Recorders were taken out of the water on 19 Aug to prevent damage to the instruments.

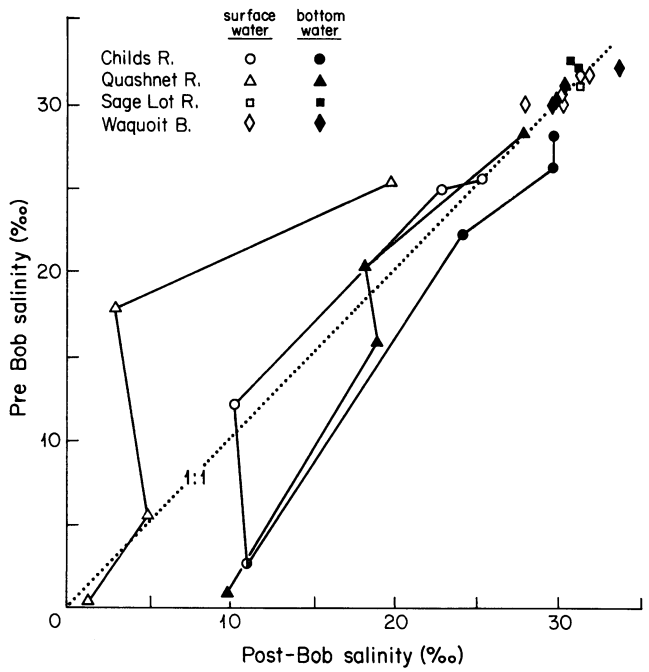

Figure 14. Salinity in water column of four sites within the Waquoit Bay system (*cf.* Figure 1 bottom right), plotted as values before passage of Hurricane Bob versus salinities just after the storm. The dashed line shows the positions values would have if no change had taken place.

The effects of the storm on salinity up and down the estuaries are best seen in Figure 14. The storm minimally altered the saltier parts of the Bay itself, Sage Lot Pond, or the saltier end of the estuaries (Figure 14). Freshening of surface water, and increased salinity of bottom water were more evident in parts of the estuaries characterized by intermediate salinities (5–20‰) (Figure 14).

Mixing of the water column prompted by the storm quickly dissipated, to be followed by a modest increase in stratification. The stratification produced by the storm lasted for a few days, presumably the interval needed to mix and discharge the saltier contribution of the surge. This fast re-establishment of previous conditions was surprising, and invited estimates of freshwater residence time. We estimated water renewal using a modification of a 2-dimensional numerical hydrodynamic model (ISAJU *et al.* 1985). The model is driven by surface gradients, bottom friction, advection, Coriolis force, and water sources. It vertically averages finite differences to simulate tidal and freshwater circulation. The model yielded residence times of 2–3 d for the whole of Waquoit Bay. These estimates are well within the recovery interval from the whole-ecosystem disturbance created by Bob. The residence time of the Quashnet River estuary is less than 1 d, indicating that it should have relaxed back from the strong forcing conditions almost as rapidly as the storm abated. The freshwater anomaly following the storm resulted from increased freshwater discharge from the watershed rather than by trapping of freshwater in the estuary.

The fast water turnover time suggested by the Bob data, corroborated by the model results, is an observation of considerable importance, since it poses problematic issues for our understanding of the biology of these systems. For example, how can phyto- and zooplankton survive, and indeed, show responses to nitrogen loading to specific subestuaries within the Waquoit Bay system, in waters whose renewal rates may be faster than biological growth and reproductive rates? How does water residence time within an estuary interact with rate of nutrient loading received from watersheds? The latter is a key issue in establishing threshold critical loads to receiving waters, a matter of considerable importance in managing water quality.

Barrier Bar Breach

Cape Cod barrier beaches have been subject to storm breaches and human intervention for a long time. Hurricanes breached the bar separating Waquoit Bay and Vineyard Sound in 1938 and again in 1944 (DEWALL *et al.*, 1984; AUBREY *et al.*, 1993). Hurricane Bob created a new channel into Waquoit Bay, eroding part of the barrier beach in Washburn Island (Figure 15). The new channel created by Bob is located in the position of the original outlet to the Eel Pond estuary of Waquoit Bay, a site that had been filled as part of a navigation management plan. This new channel remains open as of late 1996, and has had some local subsequent effects.

Circulation Changes

The new breach altered circulation only on a local scale of several ha (Figure 16). We again used the numerical hydrodynamic model of ISAJI *et al.* (1985) to simulate circulation

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Figure 15. Aerial views of the southern end of Waquoit Bay, showing the breach created by Hurricane Bob, to the right (East) of the navigation channel on Eel River, one of the two inlets into Waquoit Bay that existed before Bob. The top view was taken soon after passage of the storm, the middle during 1992, and the bottom view during 1993.

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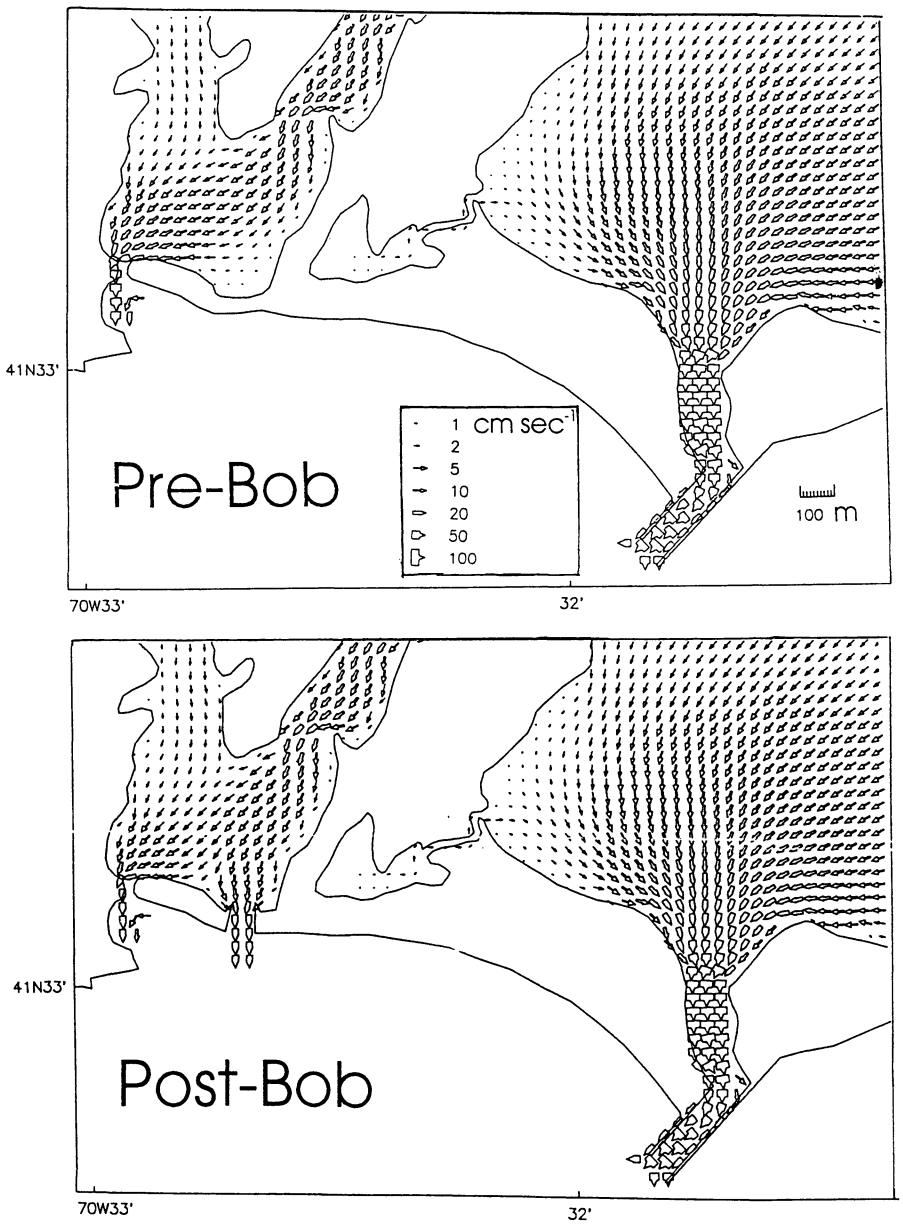

Figure 16. Water flow calculated by the model of ISAJI *et al.* (1985) for ebbing tides before (top) and after (bottom) Bob opened a new breach in the barrier bar. Data for entire Bay, and for flooding tides not shown, since no alterations were evident in either case. Arrows indicate the direction and magnitude of water velocity. Location of this detail map is the lower left of bottom right inset, Figure 1.

within Waquoit Bay before and after Bob opened the third inlet into the Bay. There were local effects within a few 100 m near the breach; the new inlet captures much of the flow between Waquoit Bay and Vineyard Sound in the south end of Eel Pond (Figure 16). Even though the new breach added 18% to the cross-sectional area opening to Vineyard Sound, there were no meaningful changes in the flow regime of the entire Bay as a result of the breach; about the same exchange rates are simply taking place through 3 rather than 2 inlets. The new inlet increased tidal range, but by less than 1% (Table 2). Residence time of water within the Bay and its estuaries also decreased, but the changes were less than 1% (Table 2).

These results have important applied consequences, because they imply that enlarging inlets by dredging may not be a practical means to alleviate eutrophication of shallow embayments such as those of Waquoit Bay. Such management actions seem unlikely to significantly enhance water exchange, at least in multiple-inlet situations similar to those in Waquoit Bay.

Beach Erosion Changes

The new channel was associated with accelerated rates of erosion of the beach on the separating Waquoit Bay and Vine-

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Table 2. *Estimated tidal amplitude and water residence time in Waquoit Bay for pre-Bob and post-Bob conditions.*

	Pre-Bob	Post-Bob	% difference
Tidal amplitude (expressed as tidal range/2, in cm)	24.78	24.84	+0.24
Residence time (hr)	45.50	45.42	−0.18

yard Sound. Historical rates of beach loss in that localized area were on average 2 m yr^{-1} (McCormick, 1994). Post-Bob rates of beach loss increased significantly; in 1993 rates of beach recession ranged between 7 and 27 m yr^{-1} (unpublished data, R. Crawford). Rates of beach loss have been slower since then.

Habitat Effects

Sand transported by the hurricane, plus subsequent further transport, obliterated eelgrass beds formerly occupying the subtidal littoral shore on the Eel Pond side of the barrier bar. This added to the loss of valuable eelgrass habitat that has been caused by nitrogen loadings from the watershed (Valiela *et al.*, 1992), and further decreased the habitat suitable for commercially important species such as scallops. The new inlet has also slowly led to erosion of dune habitats on the old spit, now changed to an island. About 18 mo after Hurricane Bob, erosion of dunes was sufficient to eliminate stands of *Rosa rugosa*, the beach rose, the major plant cover of the dunes in the area. Beach rose stands supported, among other fauna, a population of meadow voles (*Microtus pennsylvanicus*), that has since disappeared. The changes in eelgrass and dune vegetation do show some protracted, albeit local, consequences of the new breach caused by the hurricane.

Effects on Nutrients in Water and on Phytoplankton

Second-order effects of Hurricane Bob on the aquatic ecosystem of Waquoit Bay included increased nutrients in water. In turn, the enrichment was responsible for third-order effects including a phytoplankton bloom.

Increased Ammonium in Water

A pronounced peak in ammonium content of the water of Waquoit Bay immediately followed passage of Hurricane Bob (Figure 17 top). Ammonium in Waquoit Bay is predominantly generated by decay of organic matter in the benthos. Large concentrations of ammonium (reaching into the 100s of μM) occur in the water within the seaweed canopy that overlies the sediments of Waquoit Bay (Bierzychudek *et al.*, 1993). During the storm the seaweed canopy, as already mentioned, was thoroughly disturbed, so that the nutrients previously held within the canopy were mixed up into the water column. Using data on area and depth of the seaweed canopy (Hersh, 1995), and an estimate of intracanopy water volume (83% of canopy volume), we roughly estimate that mixing of intracanopy water into the rest of the water column could have increased ammonium in the water to 6×10^4 μM m^{-2}. Thus, mixing of the seaweed canopy could have easily supplied the

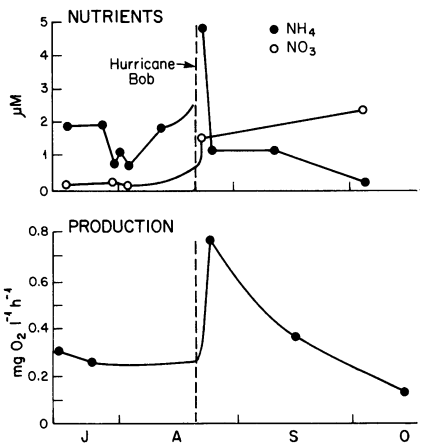

Figure 17. Ammonium and nitrate concentrations (top), and rates of phytoplankton gross production (bottom) in waters of Waquoit Bay before and after Hurricane Bob.

measured increase in ammonium evident after Bob (Figure 17 top). We conjecture that the rapid reduction of ammonium seen soon after the post-Bob peak was the result of uptake by algae, plus export to deeper waters prompted by the short water residence times in Waquoit Bay.

Only small amounts of nitrate (Figure 18 top) appeared immediately after Bob, because there is little nitrate in the intracanopy water (Bierzychudek *et al.*, 1993). The intracanopy water is anoxic a few cm below the top of the canopy, and hence contains little nitrate. Subsequent increases in nitrate seen later in the year (Figure 17 top) are typical of the seasonal pattern seen in Waquoit Bay under normal non-hurricane years (WBLMER data).

Increased Phytoplankton Growth

Phytoplankton bloomed soon after the passage of the storm. Phytoplankton production increased more than twofold for a brief period and subsequently decreased (Figure 17

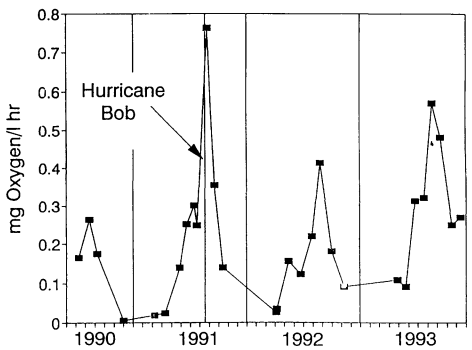

Figure 18. Seasonal pattern of gross phytoplankton production over 4 years. Ticks on x axis show month intervals. Data are averages of two depths and two sites for each of three estuaries (Childs River, Quashnet River, and Sage Lot Pond) for each date. Oxygen measured by high precision Winkler titration (Friederich *et al.* 1991).

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bottom). The post-Bob bloom stands out as a notable outlier from the apparent slow but uniform secular increase in peak phytoplankton production that we have been describing for Waquoit Bay over several years (Figure 18).

Three lines of evidence suggest that the post-Bob pulse in phytoplankton production was caused by the increased ammonium liberated from the benthic macroalgal canopy by wind-induced vertical mixing of the water column. First, we had been carrying out nutrient enrichments in 2 liter containers; these experiments showed that nitrogen additions increased growth of phytoplankton (TOMASKY *et al., submitted*). Second, a process-based WBLMER simulation model (KREMER *et al., in preparation*) predicts nitrogen limitation for phytoplankton during summer; when warm temperatures raise the potential phytoplankton growth rate high enough to overcome losses due to water exchange, the phytoplankton may grow fast enough to use all available nitrogen. The model suggests, as do the enrichment data, that during such periods, additional pulses of available nitrogen will produce phytoplankton bursts. Third, nutrients released into the water column following anoxic events stimulate short-lived blooms of phytoplankton growth (VALIELA *et al.*, 1992). In all these results, increases in water column ammonium were followed by increased phytoplankton growth. From these various results, we infer that the nitrogen made available by the storm mixing was responsible for the ecosystem-level pulse of production seen after passage of the hurricane.

The enrichment experiments, model results, anoxic event data, and the disturbance by Bob also make possible comparisons of the response of the phytoplankton at widely different spatial scales. The enrichment results pertain to scales of liters of water held in containers, so that water physics did not intervene. Anoxic events occur in parcels of water 100s of meters in diameter, parcels exposed to wind and tidal forcing. The whole-Bay response to disturbance produced by the hurricane constitutes a regional, km-scale experiment, in a water body subject to extraordinary physical forcing. The response of phytoplankton to enhanced available nitrogen was similar, independent of scale: Waquoit Bay phytoplankton thus seem largely nitrogen-limited, at liter or whole Bay scales. The similarity of the results suggests that upscaling from results of liter-scale experiments to larger spatial scales therefore seems appropriate. The nutrient-phytoplankton links appear to determine the peak response, at least in time scales of hours to a few days, despite the considerable differences in physical forcing in the different data sets.

The pulse in phytoplankton production recorded after Bob only lasted for several days (Figure 17 bottom). Uptake of nutrients by macroalgae (see below), combined with the rather short water residence times, and consequent export of nutrients as well as cells, apparently conspire to make the blooms short-lived.

Effects on Benthic Macrophytes

In spite of the disturbance created during passage by Bob, plants and macroalgae within Waquoit Bay survived Bob well. We assessed short-term effects on abundance, respiration, and nitrogen content of benthic macrophytes.

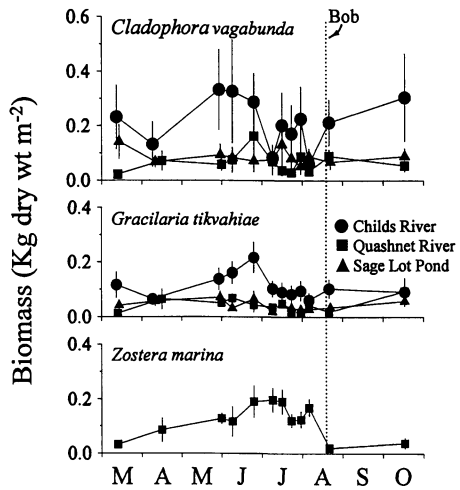

Figure 19. Biomass of the two major species of macroalgae and of eelgrass pre- and post-Bob in three estuaries of Waquoit Bay. Differences in biomass and cover among estuaries are caused by different rates of nitrogen loading to the estuaries. These data are part of a longer series reported in HERSH (1995).

Abundance

Much of the periphery of the SE of Waquoit Bay is garlanded by a saltmarsh fringe dominated by *Spartina alterniflora*. The salt marsh showed no evidence of damage at all. Although Figure 12 (bottom) shows only a single site of unaffected salt marsh, there was no real damage to saltmarsh stands visible anywhere along the shore of Waquoit Bay. The mat of interwoven rhizomes, roots, and peat, and the flexible shoots seem to have readily absorbed the forces of water, wind and flooding. There was little or no erosion of vegetated banks where there was *S. alterniflora*. Such resistance to severe storms has also been reported in the case of South Carolina salt marshes (GARDNER *et al.*, 1991), and seems to be a general feature. These strips of wetland vegetation not only survive storms well, but by their presence stabilize coastal sediments even under severe physical disturbance.

Macroalgal abundance was not affected by Bob (Figure 19 top two panels). Most seaweeds on the bottom of Waquoit Bay lack holdfasts, and merely lie on the bottom, forming a canopy that averages 10–15 cm deep, but in certain places may reach 75 cm (VALIELA *et al.*, 1992). As already indicated, we conclude that the algal canopy was thoroughly mixed up into the water column by the hurricane's winds, but the fronds quickly fell back onto the bottom after Bob passed, with little loss of biomass.

In contrast to the lack of effects on macroalgae, the hurricane removed most of the above-sediment shoots and leaves of eelgrass (*Zostera marina*) (Figure 19 bottom). The attached plants, unlike the holdfast-less macroalgae, are most affected by the storm. Similarly, attached and rigid structures such as corals can be severely damaged by storms (WOODLEY *et al.*, 1981). The array of macrophyte producers found in shallow temperate bays, such as Waquoit, seem less prone to suffer from storm damage than those where seagrasses or coral

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Table 3. *Respiration rates (means ± std. dev.) for the macroalgae* Cladophora vagabunda *and* Gracilaria tikvahiae *in two estuaries of Waquoit Bay, before and after passage of Hurricane Bob (19 Aug 1991).*

Species	Estuary	Respiration Rates (mg O_2 g DW^{-1} h^{-1})		
		1 Aug	22 Aug	14 Sep
C. vagabunda	Childs River	1.1 ± 0.2	2.9 ± 0.4	1.2 ± 0.1
	Sage Lot Pond	1.1 ± 0.2	5.3 ± 1.1	1.0 ± 0.2
G. tikvahiae	Childs River	1.2 ± 0.2	1.9 ± 0.5	1.3 ± 0.1
	Sage Lot Pond	1.2 ± 0.2	1.4 ± 0.7	1.5 ± 0.3

Table 4. *Nitrogen content (mean ± std. dev.) in the macroalgae* C. vagabunda *and* G. tikvahiae *from Childs River and Sage Lot Pond before and after passage of Hurricane Bob on 19 Aug.*

Species	Estuary	Nitrogen content (mg N g DW^{-1})		
		15 August	21 August	t test between dates
C. vagabunda	Childs River	38.7 ± 5.1	43.7 ± 4.2	Not significant
	Sage Lot Pond	31.5 ± 4.8	31.0 ± 1.4	Not significant
G. tikvahiae	Childs River	19.4 ± 0.3	23.3 ± 0.3	*
	Sage Lot Pond	14.8 ± 1.3	20.9 ± 0.6	*

predominate. We should note that even the removal of above-sediment seagrass biomass did not seem to affect the eelgrass beds in the longer term. Regrowth from the perennial roots and rhizomes of eelgrass was normal the season after the hurricane, in spite of the complete loss of leaves during the storm (HERSH, 1995).

There were no major accumulations of eelgrass or of macroalgae as beach wrack anywhere on Waquoit Bay following Bob. The slightly negative buoyancy of the macroalgae appears to have allowed them merely to fall back onto the bottom; this suggests that horizontal advection was much less important than vertical mixing during the storm. The fragments of eelgrass probably floated to the surface, since air spaces in eelgrass leaves make them buoyant, and the ebbing tide following passage of Bob, aided by the outflow of the storm surge, seem to have carried the eelgrass fragments out to Nantucket Sound.

Respiration

The two dominant macroalgae showed contrasting physiological responses to passage of Hurricane Bob. Respiration by *Gracilaria tikvahiae* was unaffected by the violent mixing associated with the hurricane. In contrast, respiration rates of *C. vagabunda*, an even more abundant macroalga in Waquoit Bay, were raised 3–5 fold after passage of the storm (Table 3). We are unsure as to the mechanism behind the rise in respiration, but stirring of the water in which the macroalgae grow raises respiration rates of the fronds (LITTLER, 1979; PECKOL and RIVERS, 1995). Sage Lot Pond is, by virtue of location (Figure 1) and topography, more exposed to on-shore winds than Childs River, which may account for the higher respiration in Sage Lot Pond (Table 3).

The higher respiration rates of *C. vagabunda* created substantial oxygen demand. For instance, with average biomass of 300 and 40 g m^{-2} of *C. vagabunda* in Childs River and Sage Lot Pond, post-hurricane respiration by macroalgae consumed 1 or 0.2 g O_2 m^{-2} hr^{-1}, respectively, in the two estuaries (PECKOL and RIVERS, 1995). The temporarily increased respiration rates translated into a nearly 50% decline in net primary production compared to summer values (PECKOL and RIVERS, 1996), clearly lowering the ratio of gross production (Pg) to respiration (R). The usual situation is for Pg:R to be well above 1, indicating net autotrophy for *C. vagabunda*. Just before the hurricane, for example, Pg:R values were 2.6 and 3.4 in Childs River and Sage Lot Pond, respectively. In both estuaries, Pg:R fell below 1 immediately after Bob. This condition probably lasted a few days at most, since respiration rates returned to normal by the middle of September (Table 3), and moreover, *C. vagabunda* recovers readily from mechanical disturbances (PECKOL and RIVERS, 1995).

Nitrogen Content

The mixing of macroalgae into the aerobic, nitrogen-enriched water column increased nitrogen content of one dominant macroalgal species but not in the other (Table 4). Normally, both species grow in a canopy that is largely in anoxic water (BIERZYCHUDEK *et al.*, 1993; D'AVANZO and KREMER, 1994); there *C. vagabunda* has an advantage, in that it is better able to take up ammonium than *G. tikvahiae* under anoxic and dark conditions. This probably accounts for the normally greater N content of *C. vagabunda* relative to that of *G. tikvahiae* (Table 4). Under aerobic conditions, nitrogen uptake by *G. tikvahiae* is 1.4 mg N gDW^{-1} hr^{-1}, about twice the rate of nitrogen uptake by C. vagabunda, 0.8 mg N gDW^{-1} hr^{-1} (PECKOL *et al.*, 1994). Thus, *G. tikvahiae* could have more readily increased its nitrogen content by uptake of the ammonium made available by the disturbance during Bob. Presumably, the lower nitrogen uptake rates of *C. vagabunda*, plus its nitrogen sufficiency even under anoxic conditions, could explain the lack of change in tissue nitrogen after Bob. Similarly, *G. tikvahiae* from Childs River, the estuary receiving higher nitrogen loads from its watershed (VALIELA *et al.*, 1992) showed higher pre-storm tissue nitrogen contents than the macroalgae from Sage Lot Pond, an estuary receiving a much lower nitrogen loading rate (Table 4). Uptake rates in *G. tikvahiae* also showed a correspondingly lower response to elevated water column nitrogen concentrations (Table 4).

Nitrogen content of both macroalgal species, and the effect of stirring from Bob, were more marked where external nitrogen loads were higher (Table 4). The pre-Bob N content of Childs River macroalgae was higher than that of Sage Lot Pond macroalgae (Table 4). The most nitrogen-depauperate *G. tikvahiae* were found in Sage Lot Pond, the estuary that receives a relatively low N loading rate from its watershed (VALIELA *et al.*, 1992). Accordingly, we found that indeed *G. tikvahiae* from Sage Lot Pond showed the largest increase (6.1 mg N g DW^{-1}, compared to 3.9 mg N g DW^{-1} in macroalgae from Childs River) in nitrogen content as a result of the Bob disturbance (Table 4). The nitrogen content in fronds of *G. tikvahiae* from that estuary did not reach that of algae

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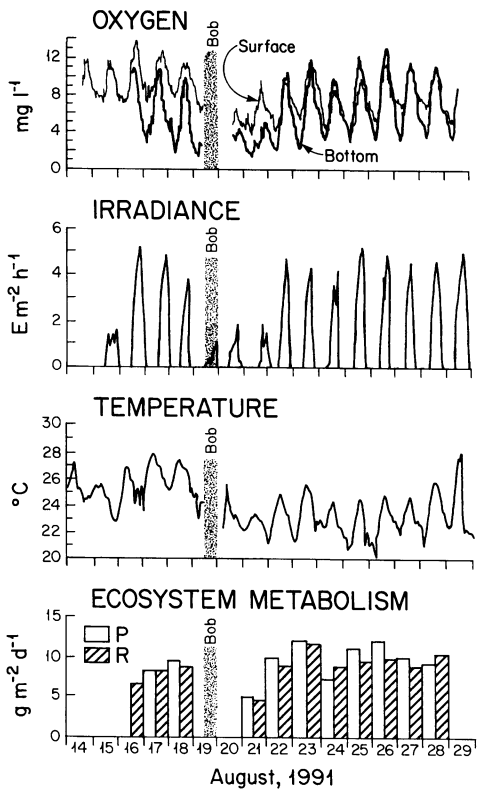

Figure 20. Oxygen (top), daytime net ecosystem production and night respiration (middle), and irradiance (bottom) in water of Childs River before and after the storm.

from Childs River, perhaps because there was much less ammonium in the intercanopy water of Sage Lot Pond.

Effects on Aquatic Animals

Aquatic animals seemed largely unaffected by the hurricane. We did find a few scallops cast ashore (Figure 12 right), but no other accumulations of dead animals were in evidence immediately or soon after the storm. Some storms may cause animal mortality, judging by reports of dead fish coming ashore after Hurricane Andrew in August 1992 in Louisiana. The fauna of the algal canopy and the littoral shores of Waquoit Bay seem likely to tolerate mixing of the water column, which may happen not infrequently (GEYER, 1997).

Effects on Total Ecosystem Metabolism

Hurricane Bob showed minor and ephemeral effects on either net daytime ecosystem production, or night ecosystem respiration (Figure 20 fourth panel). We calculated total production and total consumption of O_2 using continuous records of oxygen concentration in water of Waquoit Bay (Figure 20 top), plus measurements of gas exchange across the sea-air interface (D'AVANZO and KREMER, 1994). These data can be converted into estimates of net daytime ecosystem production (NEP) and net nightime ecosystem respiration (NER). These results in turn can be used to assess the balance between production and consumption of organic matter in whole ecosystems.

In Waquoit Bay, oxygen content of water is largely dominated by the balance between producer photosynthesis relative to respiration by macroalgae plus microbes (D'AVANZO and KREMER, 1994). The day-to-day balance between production and consumption of O_2 is largely driven by irradiance; cloudy days result in lower oxygen concentrations, bright days increase oxygen content. Irradiance was relatively low (Figure 20 second panel), and water temperatures were high (Figure 20 third panel) during and shortly after Bob. These conditions are likely to have lowered oxygen in the water (Figure 20 first panel).

By two days after Hurricane Bob, NEP had returned to levels comparable to pre-Bob conditions (Figure 20 fourth panel). We lack oxygen data, and hence metabolism estimates, for 19 Aug because we removed our oxygen sensors from the water during the storm, for fear of losing the equipment. NEP was lower during 21 Aug (Figure 20 fourth panel). This reduction is not likely to be a result of damage from the hurricane, but rather the result of low irradiation during 19–21 Aug, which lowered photosynthesis, and hence also reduced concentrations of oxygen in the water.

Net nightime ecosystem respiration was lower on 21 Aug., but two days after the storm, NER had returned to pre-Bob levels. The lowered respiration could have been caused by the somewhat colder water temperatures after Bob (Figure 20 third panel). We can examine this possibility by a graph of NER vs. temperature (Figure 21 bottom). There was a 3–4 °C drop after Bob, with a corresponding drop in respiration. Even though the water temperatures were lower after passage of the storm, NER was higher in the days following Bob. The increase in NER due to water temperature should have been from 4.5 g m^{-2} d^{-1} on 21 Aug. to 6 g m^{-2} d^{-1}, based on the increase in temperature from 23.3 °C on 21 Aug. to 25–26 °C on 22–28 Aug. (Figure 21 bottom). An additional rise in NER after Bob could have been caused by the increased respiration of *C. vagabunda* (Table 4). That increase could have contributed 7 g m^{-2} d^{-1} in NER, an estimate obtained using respiration data from Table 3, biomass data from Figure 19, and considering macroalgal respiration during the night. If we then add the 7 g m^{-2} d^{-1} to the 6 g m^{-2} d^{-1} interpolated for the 25–26 °C range in temperature from Figure 21, we find that NER should have been 13 g m^{-2} m^{-2} d^{-1}. This value is close to what was observed.

The changes in NER seen after the hurricane are therefore well within what we would predict from the known temperature change, and increased respiration by macroalgae. The apparent importance of macroalgal respiration reinforces the general point made by D'AVANZO *et al.* (1996) that in shallow systems such as Waquoit Bay, respiration by the dominant producers may be a rather large proportion of total ecosystem metabolism.

DISCUSSION

Hurricane Bob was a storm of moderate intensity (Figure 5), but even so, its passage over Cape Cod intensively disturbed aquatic and terrestrial ecosystems (Table 5). The mix-

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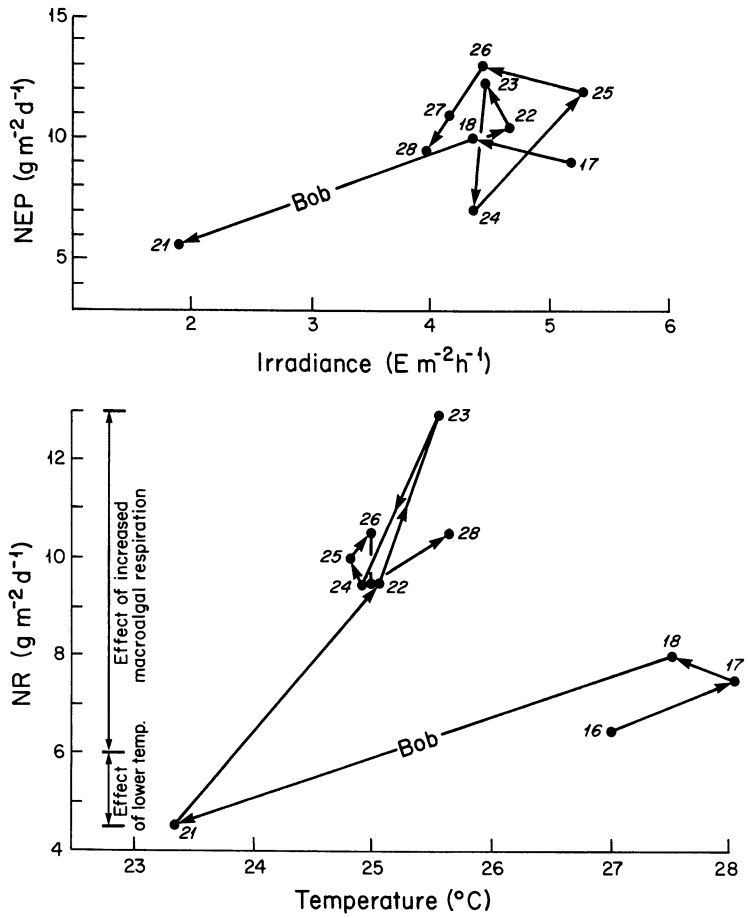

Figure 21. Relationship (and time course) between irradiance and net ecosystem production during day (top), and temperature and night ecosystem respiration. Data cover a period before and after passage of Hurricane Bob; numbers are the dates on which data were obtained.

ing of water columns, for example, completely disrupted the vertical distribution of producers and nutrients in Waquoit Bay. This disruption created a series of higher-order effects that altered respiration, production, and nutrient uptake by the aquatic producers. On land, the storm wind and salt spray disrupted forest canopies, killing tree foliage, herb layers, disturbing invertebrates, and increased leaching of ammonium from soils.

The effects of Hurricane Bob pointed out a variety of questions that merit new attention. These new aspects ranged from specialized details such as the nesting behavior of certain hornets (at variance with the entomological literature), and the stimulation of unexpected off-season blooming by exposure to salt, to larger-scale issues, such as the interaction between water residence time and primary production in estuaries. The surprisingly rapid reestablishment of stratified water columns prompts questions about how organisms maintain populations in waters with residence times of less than a day. Larger-scale still is another feature illuminated by the Hurricane Bob data, the direction of the couplings between land and sea. Generally coupling between land and sea is thought of as asymmetrical, with the land providing nutrient inputs to the sea. The hurricane results showed mechanisms by which the sea may influence adjoining terrestrial systems via salt spray. Recursively, however, salt transport to land potentially increases transport of soil nitrogen to the sea. Further, the more damage to vegetation takes place, the larger the pool of organic matter available from decay, and hence the more ammonium that may percolate through the soil, to be nitrified, and eventually to have the nitrate enter the aquifer or surface waters. In the longer term, the ammonium release should decrease as the soil-plant system recovers during the years after a major storm. The time-steps separating passage of different hurricanes may partly determine the magnitude of the pool of adsorbed ammonium in coastal forest soils. The frequency of such catastrophic disturbances might exert some influence on not only plant production and soil organic matter accumulation, but also on the N-retentive capacity of coastal watersheds. At even longer time steps, if global changes in atmospheric conditions alter frequency of large storms, notable shifts in the coupling between coastal forests and adjoining receiving waters may be in store.

Although Hurricane Bob created intense disturbances, recovery was surprisingly rapid (Table 5). The thorough hydrographic initial mixing largely disappeared within a day or so.

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Table 5. *Summary of effects on terrestrial and aquatic components, in terms of relative intensity (1: slight, 1: moderate, 3: intense), areal extent [1: local (a few ha), 2: intermediate, 3: regional], and time to recovery from the disturbance caused by Hurricane Bob.*

Effects	Mechanism	Intensity of Effect	Areal Extent	Recovery from Effect
Terrestrial:				
Tree mortality	Wind	1 (<3%)	3 (more than 7 km from shore)	Decades
Tree mortality	Salt water flooding	3 (100%)	1 (a few ha)	Years
Tree defoliation	Wind and salt spray	3 (near 100%)	3 (more than 7 km from shore)	Months
Herb mortality	Wind and salt spray	3	3 (more than 7 km from shore)	Years
Disturbances to invertebrates	Tree damage	3	3	Years
Disturbances to vertebrates	Tree damage	1	2	—
Leaching of NH_4	Salt spray	2 (25% increase in atmospheric N delivered through forests).	2 (areas beyond the nearshore)	Decades
Beach erosion	New breach	1	1	Years
Habitat effects	New breach	1	1	Years
Aquatic:				
Water column mixing	Wind stress	3 (complete mixing)	3 (whole Bay)	Hours
Barrier breach	Wind	—	1 (a few ha)	Years
Circulation	New breach	1	1	Years
NH_4 in water	Stirring of algal canopy	3 (3× increase)	3 (whole Bay)	Day
Phytoplankton bloom	Increased NH_4 in water	3 (2–3× of primary prod.)	3 (whole Bay)	Days
Eelgrass biomass	Wind stress	2 (removal of leaves)	3	Year
Macroalgal N	Release from anoxia	2 (some species)	3	Weeks
Macroalgal respiration	?	2 (2× increase)	3	Weeks

The marked effects on phytoplankton and macroalgae vanished after a few days. Some effects had longer recoveries, for example, eelgrass biomass only returned to normal after the next growing season, and hornet abundance was lower in Cape Cod for several years. Hurricane Bob did have a few long-term effects, but these seem of minor magnitude and local extent (Table 5). The new breach in the barrier bar has lasted for 5 years, but its consequences apply only to a small local area. The leaching of ammonium from soils will be having an effect for perhaps 70 years, but the increased nitrogen delivery is likely to be modest compared to increases in anthropogenic sources (SHAM *et al.*, 1994, COLLINS *et al.*, *submitted*).

In general, for both terrestrial and aquatic components, the more intense effects were also the more ephemeral (Table 5). Moreover, there were ecosystem-related differences: recovery times were mostly hours to days in the case of effects on aquatic components, while recovery from disturbances to terrestrial components were more protracted, months to decades (Table 5). These ecosystem differences stem from the faster turnover of organisms and water in the Bay compared to the watershed and aquifer. Differences in recovery time between aquatic and terrestrial ecosystems of the kind discussed here may have important implications for management purposes, and may also extend to responses to other disturbances such as pollutants.

To a significant extent, the kinds of organisms present in the aquatic system appear to matter. In shallow temperate estuaries we have seen that the macroalgae tolerate storm disturbance rather well, and rooted macrophytes merely bend to the wind, as in the case of the salt marsh vegetation, or regrow from below-ground parts, such as in the case of eelgrass. Rigid structures, such as those of trees and corals, make for greater sensitivity to storm damage.

The effects of Hurricane Bob permitted comparison of results obtained at different spatial scales, and suggested the appropriateness of upscaling interpretation of results of liter-scale manipulative experiments, to data on anoxic events in water masses at 10–100s m scales, and to hurricane-mediated disturbances at the regional scale of km. The comparisons allowed the conclusion that at all three spatial scales, phytoplankton respond to additions of dissolved inorganic nitrogen by increases in growth.

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