

The Changing Ecology of Temperate Coastal Waters During a Warming Trend¹

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ABSTRACT: In the temperate North Atlantic Ocean the ecological changes in coastal waters associated with a warming period in the 1930s were compared with the past couple of decades when the North Atlantic Oscillation was also positive. Long-term monitoring data sets from Rhode Island and nearby coastal waters were used to identify trends in the recent warming period. During both events winter water temperatures warmed above a mean value of 2.9°C from 1°C to 3°C. There was no apparent trend in the annual salinity cycle correlated with the increased temperature. During both periods boreal species declined, southern species increased, and widespread declines in eelgrass occurred. Estuaries on the western Atlantic Ocean during the recent warming period had phytoplankton biomass during the winter-spring bloom decrease, zooplankton number increase, and nutrients remain elevated due to enhanced zooplankton grazing. Zooplankton numbers decreased in summer due to enhanced ctenophore predation. In these waters the loss of boreal demersal fish has been compensated by an increase in demersal decapods. The very large ecological changes caused by small increases in seasonal temperature provide an insight to the large alterations that may be associated with global warming.

Introduction

The warm periods of the 1930s and 1980s to 1990s had winter water temperatures 1–3°C above average and caused changes in the ecology of north temperate coastal waters on both sides of the Atlantic Ocean (Cushing 1982; Drinkwater et al. 2003; Reid et al. 2003). In Narragansett Bay, Rhode Island, United States, the changes in the recent decades affected phytoplankton (Keller et al. 2001; Oviatt et al. 2002), zooplankton (Sullivan et al. 2001), and fish (Jeffries and Johnson 1974; Jeffries and Terceiro 1985; Keller and Klein-MacPhee 2000). In the eastern Atlantic Ocean the changes observed in the 1930s, such as increased southern species and decreased northern species, were repeated in the recent warming period (Reid and Edwards 2001; Southward et al. 1995). Scientists in the recent warming period were able to discern driving forces, such as nutrient pulses, from the North Atlantic gyre circulation to the North Sea that enhanced phytoplankton production (Southward et al. 1995; Reid et al. 2003). The 1930s observations from the British Isles (Cushing 1982), which were more detailed and widely published than the observations from the western Atlantic Ocean, provide a historical context for observations in the recent warming period.

In the British Isles scientists closely monitored the effect of the 1930s warming on marine organisms for the northeast Atlantic Ocean. During the 1920s and 1930s warm water species invaded waters around the British Isles and cold water species declined (Cushing 1982). Two species of jellyfish, the Portuguese Man-of-War (*Physalia physalia*) and By-the-Wind-Sailor (*Verella verella*), made frequent appearances. Loggerhead turtles (*Caretta caretta*) and common octopus (*Octopus vulgaris*) appeared. In the intertidal the southern Goose barnacle (*Chthamalus stellatus*) replaced the northern barnacle (*Balanus balanoides*). Benthic communities became more characterized by southern species. Northern demersal fish such as cod (*Gadus morhua*) and flatfish (several species) decreased. Eelgrass (*Zostera marina*) decreased along southwest England and Brittany. In the early 1930s the eelgrass decline occurred not only in England but also France, Holland, Spain, Portugal, Denmark, Sweden, and Norway (Rasmussen 1977). From 1924 to 1939 Sir Frederick Russel collected weekly samples of plankton in the English Channel close to Plymouth. Cushing (1982) described five trends of the Russel cycle: the winter phosphate maximum decreased; cold preferring species of fish larvae disappeared with cod-like fish (*gadoid*), flatfish, and herring-like fish (*herring*) larvae declining and pilchard (*Sardina pilchardus*) eggs increasing; macroplankton decreased by a factor of four; the southern arrow worm (*Sagitta elegans*) replaced the northern *S. setosa*; and the cycle reversed in the mid 1960s and early 1970s.

During the 1930s the economic depression lim-

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ited scientific observation to mainly commercial landings data and temperature observations in the northwest Atlantic Ocean. Drinkwater et al. (2003) described invasions of species in the Bay of Fundy and Nova Scotian waters, increases in Atlantic salmon (*Salmo salar*) and haddock (*Melanogrammus aeglefinus*), increased landings of lobster (*Homarus americanus*) in Canada, and changes in whale migration with white whales (*Delphinapterus leucas*) and narwhales (*Monodon monoceros*) arriving earlier and leaving later. Cushing (1982) described the rise of the west Greenland cod fishery. He ascribed the rise to a stronger Irminger current warming the east Greenland current to west Greenland providing new habitat to sustain cod in this region. The biggest change in the northwest Atlantic was the 90% decline in eelgrass from Canada to North Carolina (Rasmussen 1977). This 1930s decline almost certainly also occurred in Narragansett Bay (Doherty 1995). Most of the literature on the eelgrass decline attributed the decline to a wasting disease (Milne and Milne 1951). Rasmussen (1977) disagreed that the decline was due to a wasting disease and countered that the identified slime mold was part of the disintegration of dead eelgrass tissue. He noted that the decline of the 1930s coincided with warm summers and mild winters throughout its large range. He ascribed the decline to increased water temperatures on the basis that where temperature did not change, such as the Mediterranean, the beds remained healthy. This hypothesis was strengthened by a limited recovery of eelgrass beds in the northwest Atlantic occurring in the colder late 1950s to 1970s during a negative period of the North Atlantic Oscillation (NAO; Keser et al. 2003).

In the 1980s and 1990s in the northeast Atlantic, the ecological trends observed in the 1930s reoccurred with southern species increasing and northern species decreasing (Southward et al. 1995). Phytoplankton biomass in the North Sea increased by a factor of three due to nutrient pulses from increased circulation of North Atlantic water (Reid et al. 2003). Benthic biomass of animals increased with increased primary production (Reid and Edwards 2001). Large-scale changes occurred with respect to calanoid copepods. A northward extension of more than 10 degrees of latitude was detected in continuous plankton recorder data for the assemblage of warm water species and there was a corresponding decrease in the number of cold water species to the southwest of the British Isles (Beaugrand et al. 2002). Their analyses indicated a strong shift in the northeast Atlantic marine ecosystems toward a warmer dynamic equilibrium.

In the 1900s two positive periods of the NAO, from the 1920s to the 1930s and from the 1980s

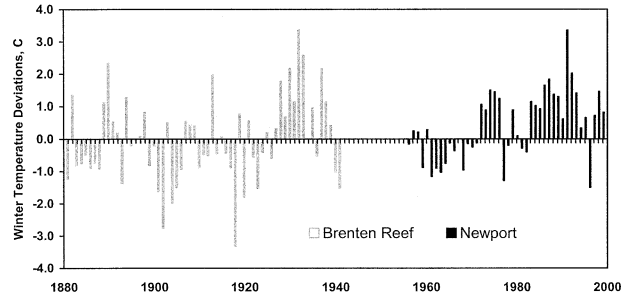


Fig. 1. Winter water temperature deviations in degrees Centigrade from the mean at the Brenton Reef Light Ship prior to 1939 and from Newport Harbor after 1955. No data was available for the interval between the two data sets. Mean temperature was 2.9°C for the record, 2.7°C for Brenton Reef, and 3.1°C for Newport.

to the 1990s, sandwiched a negative period during the 1950s and 1960s. The NAO is most pronounced during winter and its index is based on sea level pressure differences between the North Atlantic at Iceland or Greenland and the mid Atlantic at Lisbon, the Azores, or Gibraltar (Hurrell 2003). The NAO is the Atlantic expression of the larger hemispheric change in the westerly winds including the jet stream. Simultaneous changes occur in the Atlantic and Pacific Oceans and these hemispheric changes are the Arctic Oscillation (Corti et al. 1999). During the positive NAO phase the pressure difference between the sites is large; during a negative phase, such as the 1950s to the 1960s, the pressure difference between sites is small. The positive NAO causes strong westerly winds that result in warm winters in the eastern U.S. and over Europe. During this positive phase waters are warmer than usual at temperate latitudes and colder than normal in the far North Atlantic, particularly Labrador. The negative NAO results in north to south storm tracks over North America and Europe resulting in cold stormy winters. During this phase sea water is colder than normal in the far North Atlantic: Labrador, Greenland, and Iceland. In any winter high variability occurs and the NAO index does not vary on any preferred time scale. In contrast to the western Atlantic where 1977 was the only cold winter until 1996 (Fig. 1), the eastern Atlantic experienced a cold period from 1978 to 1982 and a warming period afterwards (Reid and Edwards 2001). In the recent warm period in the northwest Atlantic the cold winters of 1977 and 1996 were strong examples of a negative oscillation; warm winters of 1991, 1992, and 1998 were strong examples of a positive oscillation.

The enormous ecological changes resulting from small mean changes in winter temperature

due to the NAO lead to the examination of these shifts for patterns that reveal whether they are predictable across time (1930s versus 1990s) and geography (temperate east to west Atlantic). This paper examines the ecological changes in Narragansett Bay during the recent warming trend and compares and contrasts these changes with those observed in the 1930s in the temperate east and west Atlantic. I examined new data from Narragansett Bay (1977–2000), compared system responses with patterns from the earlier warm period, and investigated the causes and generality of these patterns across geographic boundaries. The changes observed during these warming periods will be repeated and enhanced during prolonged periods of warming associated with global warming.

Methods

TEMPERATURE RECORDS

Several long-term data sets describe the water temperature of Narragansett Bay and agree well enough to be used interchangeably. At Newport, Rhode Island, the National Oceanic and Atmospheric Administration (NOAA) measured temperature at a tide gauge station (#8452660) from 1955 to 1996 (www.noaa.gov). This hourly data is provided as monthly means and compares favorably with weekly data taken at Fox Island in the lower West Passage of Narragansett Bay by the Graduate School of Oceanography (GSO) fish trawl survey (Hawk 1998). Temperature data from Woods Hole, Massachusetts, have been taken since 1893 and are available as mean monthly temperature and compare well with Narragansett Bay temperatures (Nixon et al. 2004). At the mouth of the bay the crew of the Brenton's Reef lightship measured the temperature of the water almost daily, from July 1878 through January 1940 (Nixon et al. 2003). While this data set is more variable than bay temperature records, it provides the most complete record for the warming period of the 1930s.

GSO DOCK RECORDS

Since fall 1976 samples have been taken weekly off GSO for salinity, chlorophyll, ammonia, nitrate and nitrite, phosphate, and silicate. Samples were not collected from October to December 1977 and from April to May 1981, but these represent the only two prolonged periods of missing data for all variables. During 1977 and 1978 samples were taken by Niskin bottle from a depth of about 2 m; after that samples were taken from the header tank supplying input water to the Marine Ecosystem Research Laboratory (MERL; Pilson 1985). The intake was located under the dock at GSO at a depth of 2–3 m depending on tide below the water surface. The residence time of the water in the header

tank was about 15 min and the tank was well mixed (Pilson 1985). When the laboratory ceased full operation, samples were again taken off the GSO dock beginning July 1997 to the present.

Samples for salinity were measured on an Autosal Analyzer at the NOAA National Marine Fisheries Laboratory in Narragansett, Rhode Island.

Samples for chlorophyll *a* were measured according to the method of Yentsch and Menzel (1963) as modified by Lorenzen (1966). Prior to July 1984, all chlorophyll determinations were performed using a Turner Model III fluorometer; subsequent determinations were performed using a Turner Designs Model 10 Series Field Fluorometer (Oviatt and Hindle 1994). In August 2002 this instrument was replaced by a Turner Design Model 700 after intercalibration of the two instruments.

Dissolved inorganic nutrient samples were analyzed using a Technicon AutoAnalyzer, based on the procedure after Solorzano (1969) for ammonium, Wood et al. (1967) for nitrite plus nitrate, Hager et al. (1972) for phosphate, and Brewer and Riley (1966) for silicate. Samples not analyzed immediately were frozen and later thawed for analysis (Oviatt and Hindle 1994).

GSO FISH TRAWL SURVEY

Since the 1950s otter trawl survey data (30 min tows: 2.5 cm stretch mesh in the cod end) have been collected weekly from a Fox Island station off Wickford in Narragansett Bay by Charles J. Fish, by H. P. Jeffries, and currently by J. Collie (unpublished data). Data from the Fox Island station represents fish populations in the mid to lower West Passage in 6–7 m of water over a silty-sand sediment (Jeffries and Johnson 1974). Trawl survey fish and invertebrate data are presented by number per tow totaled or averaged by month or year and are available on request.

RHODE ISLAND DEPARTMENT OF ENVIRONMENTAL MANAGEMENT (RIDEM) FISH TRAWL

From 1979 to the present, the RIDEM has conducted spring and fall trawl surveys (20 min tows at 2.5 knots) at about 26 stations in Rhode Island coastal waters (Lynch 2000). Distribution of sampling stations employed both random and fixed allocation. The 3/4 scale high-rise bottom trawl had a head rope length of 13.7 m, a foot rope length of 28.3 m, and cod end liner mesh of 0.95 cm. Trawl survey data were presented as number per tow and biomass per tow in kg wet weight. For some analyses data have been compiled and accumulated for type species for all stations for several year periods.

Results

TEMPERATURE AND SALINITY

The period of the GSO dock samples from 1977 to 2000 coincided with a mainly positive period of the NAO and a period of warmer than average temperatures (Hurrell 2003). The records of winter temperature from Newport and Brenton Reef have been combined to show the temperature deviations from the mean of 2.9°C from the 1870s to 2000 (Fig. 1). The warming period of the 1930s exhibits temperatures 1–3°C above the mean at Brenton Reef. For the period from 1940 to 1955, World War II interrupted the data record. The period of warming in the 1980s and 1990s at the Newport tide gauge was indicated by temperature increases of 1–3°C above the average with 1991 being the most extreme winter of warming. A lack of constancy was evident in the record. A period of positive NAO and warmer temperature began in the early 1970s and abruptly changed to a negative NAO and the cold winter of 1977. The long record of warmer temperatures in the 1980s and 1990s also abruptly switched to negative NAO and cold in the winter of 1996. During the sampling period, the prolonged warm period had occasional cold years to provide contrasting conditions for ecological changes.

In Rhode Island and Massachusetts waters the most extreme seasonal warming took place in the winter of the year and the least in the fall of the year. In Chesapeake Bay an analysis of annual average temperature from 1957 to 1998 for each month revealed a similar pattern with significant positive trends for December, January, and March–August excluding May for an annual increase of 0.7–1.8°C over that period (Wood et al. 2002). In Rhode Island and Massachusetts waters over the period of sampling the average seasonal temperature ranged from about 1°C in February, the coldest month, to 22°C in August, the warmest month (Fig. 2). During the warmest year of the record, 1991, average monthly temperatures ranged about 2°C above the mean in winter, 1°C in spring, 0.7°C in summer, and coincided with the mean in fall. During the colder year of 1996 temperature was 0.7–0.4°C below the average in January and February, 0.4–0.7°C above the record in July and August, and coincided with the average in spring and fall. The extreme monthly range in temperature for the sampling period was about 3°C in winter and 1.4°C in summer.

Mean monthly salinity at the GSO dock ranged from about 29.5 psu in April to a high of almost 30 psu in October indicating a weak seasonal signal with the lowest values in the spring and highest values in the fall (Fig. 3). The 1991 warm year had

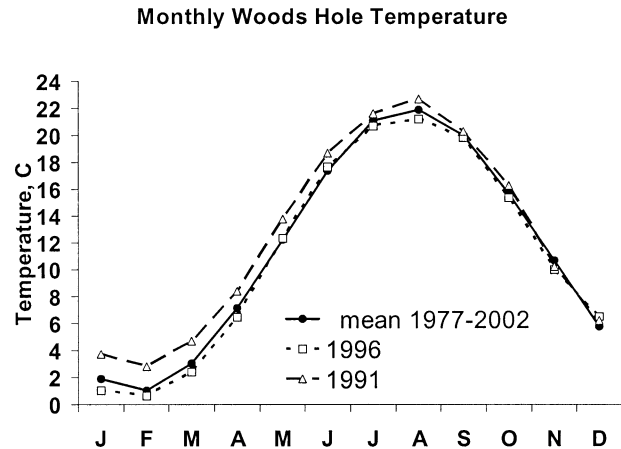


Fig. 2. Seasonal water temperature at Woods Hole, Maryland (similar temperatures to Newport, Rhode Island, prior to discontinuation of Newport record in 1996; see methods), showing the mean from 1977 to 2002 and contrasting values for 1996 (a cold year) and 1991 (a warm year).

a similar salinity pattern to the mean but generally had 0.1–0.5 psu higher values than the mean. Data for the 1996 and 1977 cold years were incomplete but generally showed variable and lower values than the mean salinity value. These slightly different patterns suggested lower salinity in cold years compared to warm years. Precipitation had been increasing over the century in Rhode Island but it has not been apparently variable with respect to NAO trends (Hawk 1998). Ten-year annual means indicate 101 cm for the warm 1930s compared to 105 cm for the cool 1960s, 124 cm for the 1970s, 114 cm for the 1980s, and 122 cm for the 1990s (Pilson 1989; www.noaa.gov).

CHLOROPHYLL AND NUTRIENTS

The mean seasonal pattern for phytoplankton biomass showed maximum values in winter and a lower maximum in summer with values ranging from 5.3 $\mu\text{g l}^{-1}$ chlorophyll in February to 2.6 $\mu\text{g l}^{-1}$ in May to 3.9 $\mu\text{g l}^{-1}$ in July (Fig. 3). The overall pattern showed little variability and the mean values showed no evidence of a fall bloom. The main difference between a cold year and a warm year was a strong winter phytoplankton bloom in the cold year with values reaching 9.5 $\mu\text{g l}^{-1}$ in February in 1996 compared to 3.5 $\mu\text{g l}^{-1}$ in 1991.

The nutrient patterns were consistent with chlorophyll patterns with maximum winter values falling lowest in the cold year compared to the warm year but nutrients also tended to decrease in the February of the warm year (Fig. 3). Generally nutrient concentrations reached maximum values in winter prior to a bloom, minimum values in spring, and increased with remineralization over the summer. Mean dissolved inorganic nitrogen (DIN)

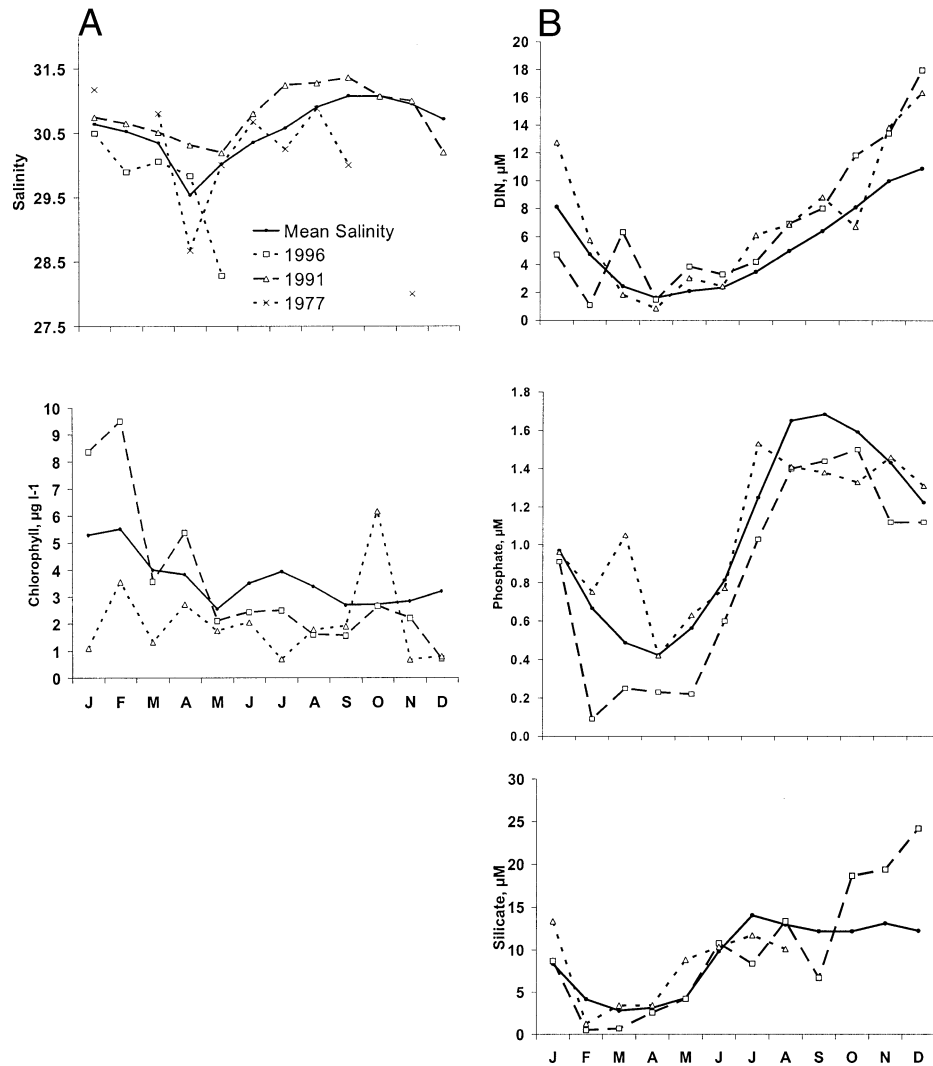


Fig. 3. Mean seasonal patterns of salinity, chlorophyll, and nutrients (dissolved organic nitrogen, phosphate, and silicate) contrasting warm and cold years. Samples were taken off the Graduate School of Oceanography dock in the lower West Passage of Narragansett Bay showing the means from 1977 to 2002 and contrasting values for 1996 a cold year (and 1977 for salinity) and 1991 a warm year.

reached a maximum value of $10.8 \mu\text{M}$ in December and decreased to a minimum value of $1.6 \mu\text{M}$ in April. From December to February DIN dropped $10.6 \mu\text{M}$ in 1996 compared to $7.4 \mu\text{M}$ in 1991. Mean inorganic phosphate reached a maximum value of $1.7 \mu\text{M}$ in September and a minimum value of $0.43 \mu\text{M}$ in April. From December to February phosphate dropped $1.22 \mu\text{M}$ in 1996 compared to $0.57 \mu\text{M}$ in 1991. Mean silicate reached a maximum concentration of $14.4 \mu\text{M}$ in July and a minimum value of $2.8 \mu\text{M}$ in March. The winter decrease in silicate values was $15.8 \mu\text{M}$ in 1996 and $12.1 \mu\text{M}$ in 1991. The ratios of nitrogen:phosphorus utilization of 9 in 1996 and 13 in 1991 suggested nitrogen limitation during the winter bloom.

During the 1980s to 1990s warm period, weak trends were evident in chlorophyll and nutrient annual means (Fig. 4). A peak in chlorophyll in 1977 can be attributed to a winter–spring bloom in that cold winter; a peak in 1985 can be attributed to the brown tide bloom that occurred that year. The picophytoplankton *Aureococcus anophagefferens* reached concentrations of $2 \times 10^9 \text{ cell l}^{-1}$ during the summer of 1985 and was too small to be grazed by macrozooplankton or bivalve filter feeders (Keller and Rice 1989). Chlorophyll appeared to drop in the early 1990s compared to earlier values during a several year period of minimal or no winter–spring bloom biomass accumulation. During 1994 and intermittently, notably in 1996, bloom biomass increased and annual values in the late 1990s also

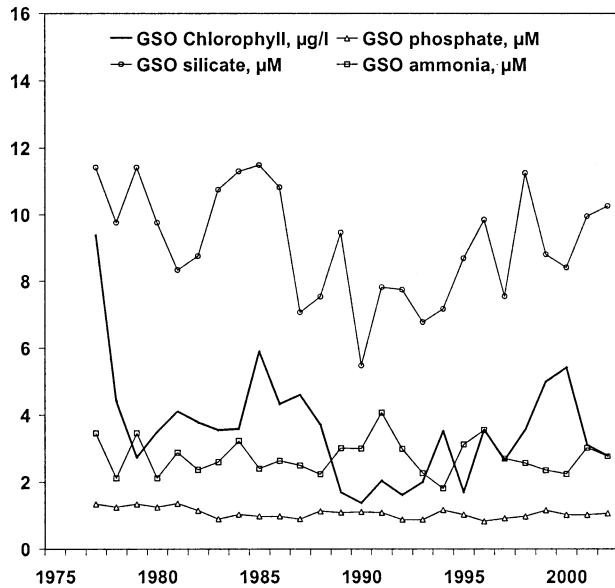


Fig. 4. Annual mean values for chlorophyll and nutrient concentrations off the Graduate School of Oceanography dock in the lower west passage of Narragansett Bay from 1977 to 2002.

increased. Dissolved ammonia responded with a weak inverse trend to chlorophyll. Phosphate showed a slight decrease over the period of the record and was decreased compared to early records of the data (compare Fig. 4 to Pilson 1985). Silicate was variable with no obvious trend relative to other variables.

FISH AND INVERTEBRATES

Northern demersal fish species declined from the early 1980s to the late 1990s; southern pelagic species had minor variations over the recent 20-yr warming period. The RIDEM trawl survey data showed a pattern of decreasing demersal fish by a factor of four and a pattern of increasing pelagic fish in the late 1980s (Fig. 5). The dominant species of demersal fish, which decreased over the 20-yr period, included the more boreal species of winter flounder (*Pseudopleuronectes americanus*) (−90%*), windowpane flounder (*Scophthalmus aquosus*) (−89%*), northern sea robin (*Prinonotus carolinus*) (−88%*), sea raven (*Hemitripterus americanus*) (−99%), and red hake (*Urophycis chuss*) (−91%*). * indicates significance at the 95% confidence level according to the Student's *t*-test. The dominant species of pelagic nekton which increased, were more southern species including bay anchovy (*Anchoa mitchilli*) (+48%*), butterfish (*Poronous triacanthus*) (+60%*), alewife (*Alosa pseudoharengus*) (+96%*) and long finned squid (*Loligo forbesii*) (+45%*). Scup (*Stenotomus chrysops*), a dominant species that was included in the pelagic

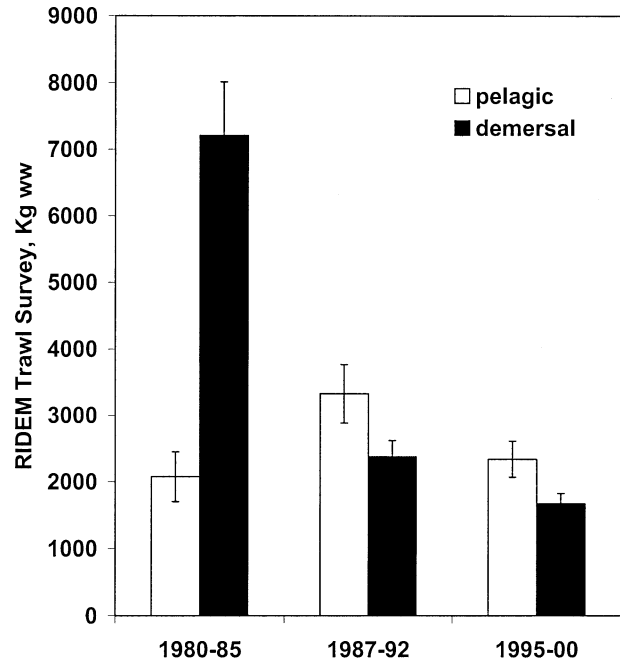


Fig. 5. Demersal and pelagic fish species cumulative biomass over 5-yr intervals at 26 stations at the beginning, middle, and end of the survey period from 1980 to 2000 from the spring-fall Rhode Island Department of Environmental Management trawl survey (Lynch 2000). Bars represent standard deviations.

fish, initially increased slightly in early 1990s and then decreased in the late 1990s. If commercially important species like winter flounder, scup, and squid were omitted, abundance declined but the pattern remained unchanged. Fishing pressure may have reduced biomass but the pattern of boreal bottom fish decreasing remains. Overall fish biomass for these selected species declined by over 5,000 kg ww or 57% in the late 1990s compared to the early 1980s, i.e., the pelagic replacements tended to be smaller fish.

The decline in bottom fish after the cold period of the 1960s was closely followed by an increase in decapods including several species of crabs and lobsters (Fig. 6). As sea robin and other bottom fish decreased in the late 1960s and 1970s, cancer crab species (*Cancer irroratus* and *Cancer borealis*), the most dominant decapods, increased in the early 1980s. If a wet weight of 150 g is assumed for lady crab (*Ovalipes ocellatus*) (based on three individuals), if 450 g is assumed for cancer crab (based on four individuals), and if 458 g is assumed for lobster (based on three individuals), then the biomass increase for decapods can be estimated at about 3,000 kg for the late 1990s or close to the magnitude of the loss in fish biomass. Lobsters showed a sustained peak abundance from the early 1990s to the late 1990s instead of the oscillating

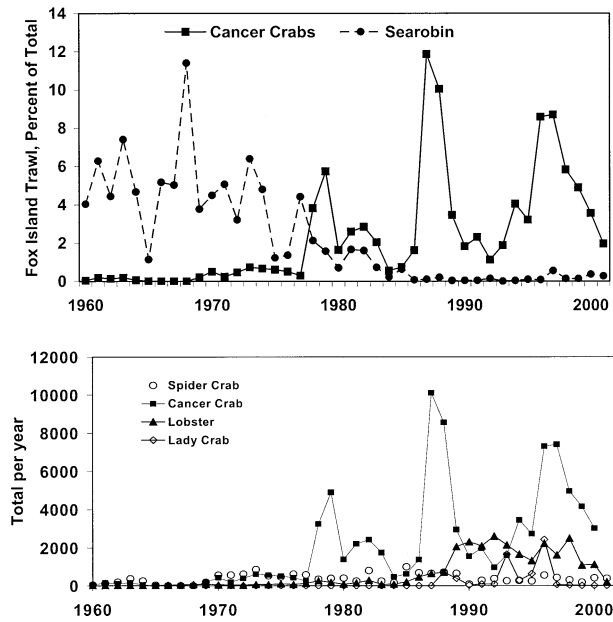


Fig. 6. The switch in dominance of boreal demersal fish to decapods as illustrated by sea robin and cancer crabs and the increase in several species of decapods from 1960 to 2001 in the Graduate School of Oceanography trawl survey at Fox Island.

abundance displayed by crab species. All decapods have apparently declined in the late 1990s although not yet to the levels prior to 1977.

Discussion

The increased winter temperatures of the 1930s and the 1980s were roughly of the same magnitude in the temperate Atlantic Ocean although the recent warming period has been more prolonged than the earlier period (Fig. 1). Similar patterns that occurred in the east and west included the northward movement of southern species, a decline in boreal demersal fish species, and widespread decline of eelgrass beds. Eelgrass beds after strong signs of recovery in the cooler 1960s again declined in New England waters during the recent warming period (Keser et al. 2003). Mesocosm experiments indicated the death of eelgrass was associated with higher temperatures and nutrients (Bintz et al. 2003). As the plants tried to grow faster in their light limited environment, respiration outstripped production leading to the most rapid declines in high temperature and high temperature-high nutrient treatments (Fig. 7). Patterns that appeared confined to the eastern Atlantic included increased phytoplankton (due to increased circulation and nutrient advection) and increased sardines and decreased herring. Although benthic fauna tended to increase in the eastern Atlantic (Reid and Edwards 2001), a pattern only evident

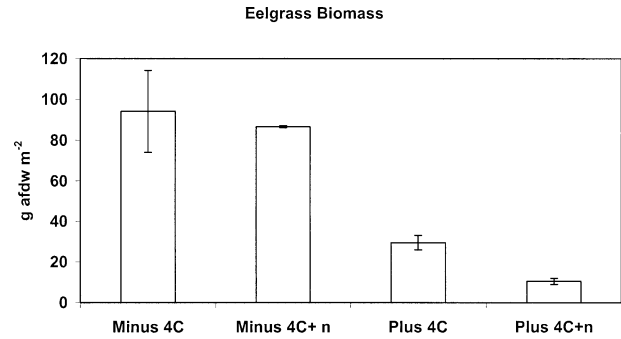


Fig. 7. Eelgrass biomass at the end of a 3-mo (June, July, and August) mesocosm (4.6 m³, 4.2 m²) experiment with temperature treatments of +4°C and -4°C from average temperatures in Rhode Island coastal lagoons and temperature and nutrient addition treatments (-4°C + n, +4°C + n) where n = 6 and 0.5 mmol m⁻² d⁻¹ of NaNO₃ and KH₂PO₄, respectively (re-drawn from Bintz et al. 2003). Error bars are standard error.

in the western Atlantic was increased decapods, including heavily fished lobster populations (Fig. 6). While no evidence of increased decapod population levels has emerged for the eastern Atlantic, the distribution of decapod crustacean larvae has been enhanced to more northern latitudes during the recent warming period (Lindley 1998). A newly discovered pattern in Rhode Island waters was zooplankton grazing control of the winter-spring phytoplankton bloom with consequences for seasonal dynamics through the rest of the year as described below (Keller et al. 1999; Sullivan et al. 2001).

One southern species, the American oyster (*Crassostrea virginica*), repopulated Narragansett Bay after an absence of four decades (Fig. 8). In the early 1990s, probably the warm spring of 1991, oysters set bay-wide (Fig. 1). Extensive bay-wide sets have only been recorded twice previously, in 1890 and 1908 during years that exhibited elevated mean annual air temperature (Kochiss 1964; Pilon 1989). Commercial exploitation began in 1996

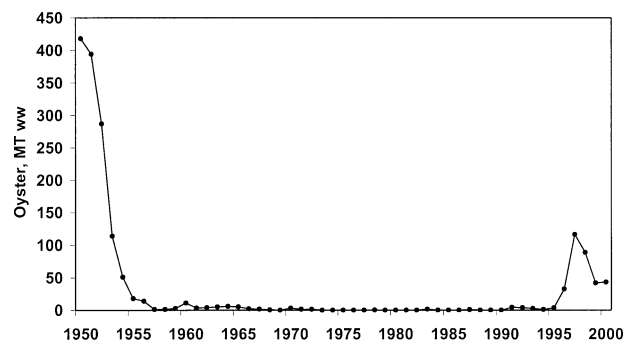


Fig. 8. Rhode Island landings data for oysters from 1950 to 2000 from the National Marine Fisheries Service (National Marine Fisheries Service unpublished data).

as oysters reached the legal size of 76 mm in Rhode Island (National Marine Fisheries Service unpublished data). During a 1998 disease survey, Dermo (*Perkinsus marinus*), a protozoan parasite, was found in 56% of the oysters recently dead (Gomez-Chiarri personal communication). Ford (1996) has suggested that this southern parasite has extended its range into the northeast in response to warmer winters.

Northern species of demersal fish decreased and were replaced by smaller, more southern, pelagic species (Fig. 5). During the 1990s the emptied demersal habitat was repopulated by decapods that may have been able to take advantage of reduced demersal fish predation and competition resulting in an increased survival of young and an increased benthic food supply (Fig. 6). The once dominant winter flounder has a strategy of laying demersal eggs in the coldest months of the year. During warmer winters predators remain active to prey on the eggs and larvae. *Crangon* shrimp have been shown to have the potential to reduce the recruitment success of winter flounder (Whitehouse 1994; Taylor et al. 2004). While winter flounder larval mortality is significantly related to the abundance of predators, such as shrimp and the mud anemone *Cerianthiopsis americana*, predation is not the only factor (Keller and Klein-MacPhee 2000). Winter flounder egg survival, percent hatch, time to hatch, and initial size improve under cool spring conditions compared to warm (Keller and Klein-MacPhee 2000).

In the northwest Atlantic and Rhode Island waters the decline of the winter-spring diatom bloom has changed the seasonal benthic-pelagic coupling (Fig. 3). The cold winter of 1996 displayed a winter-spring diatom bloom intensity, typical of negative NAO years of the 1950s and 1960s. During cold winters with a strong diatom bloom benthic infauna, particularly polychaetes, reproduce in late spring and provide prey for demersal fish (Townsend and Cammen 1988; Ellis 2002). During warm winters of the 1980s and 1990s zooplankton and benthic filter feeder grazing led to the decline in phytoplankton biomass during the winter-spring bloom period (Keller et al. 1999, 2001; Oviatt et al. 2002). While a decline in nutrients during warm winters indicated growth by phytoplankton, grazing controlled the accumulation of phytoplankton biomass. Nutrients decreased in the warm winter of 1991 even with no winter-spring phytoplankton accumulation, suggesting that as phytoplankton grew faster, zooplankton grazed faster encapsulating almost as much of the particulate nutrients into fecal pellets as fell ungrazed to the sediment in the cold 1996 winter.

The input of organic matter to the benthos must

have been altered from sinking phytoplankton to sinking zooplankton fecal pellets resulting in reduced polychaete abundance but no reduction in overall infauna abundance (Ellis 2002). Zooplankton remained active and increased in numbers throughout warmer winters in contrast to the reverse pattern observed in cold winters (Keller et al. 2001). Another change in the zooplankton community, associated with warmer temperatures, was a shift in ctenophore (*Mnemiopsis leidyi*) abundance from maximum numbers in late summer to maximum numbers in late spring (Sullivan et al. 2001). The shift in ctenophore abundance appears linked to warmer winter temperatures and increased spring zooplankton. Overwintering ctenophores in a warm winter find an enhanced copepod prey supply that stimulates growth and reproduction resulting in elevated numbers of ctenophores by early summer. The early summer heavy ctenophore predation upon zooplankton, including decapod larvae decreases summer population levels of these prey taxons and their predators, small pelagic fish. This predation may explain the decrease in pelagic fish between 1987–1992 and 1995–2000 (Fig. 5). The summer copepod populations of *Acartia tonsa*, for example, have declined to very low levels during 2000–2003 following large spring pulses of ctenophores (Sullivan personal communication). The large oscillations in the abundance of cancer crabs and the decrease of crabs and lobsters in the late 1990s may be related to high summer abundance of ctenophores in the mid 1990s (Fig. 6); the ctenophore data to support or refute this hypothesis does not exist. The decrease in summer zooplankton has stimulated summer blooms of phytoplankton, whereas in the past fall phytoplankton blooms were stimulated by ctenophore predation on zooplankton (Deason and Smayda 1982; Sullivan personal communication).

Small increases in temperature have switched temperate ecosystems into a more southern species regime and seasonality in the northeast and northwest Atlantic. These trends will surely re-occur and be enhanced during a period of global warming. The loss of boreal demersal fish species has been prominent on both sides of the Atlantic Ocean. In local waters the decrease in demersal fish biomass and secondary production has been compensated by a large increase in demersal decapods. In local New England waters a marked change was evident in seasonal patterns. The switches have been from high to low phytoplankton biomass in winter, from low to high zooplankton biomass in early spring, from high to low zooplankton biomass in summer, and from low to high summer phytoplankton biomass. Enhanced zooplankton grazing has caused the winter switch and enhanced ctenophore graz-

ing has caused the summer switch. Starting in 1996 negative NAO periods and colder temperatures have become more frequent in winter (Fig. 1). The recent colder winters may suggest a climate trend, perhaps reduced in intensity, trying to return to a period more like the 1960s in the western Atlantic.

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