



Change in body size in a rapidly warming marine ecosystem: Consequences of tropicalization

Kevin D. Friedland^{a,*}, Laura C. Ganley^b, Donna Dimarchopoulou^{c,d}, Sarah Gaichas^e, Ryan E. Morse^{a,f}, Adrian Jordaan^g

^a Northeast Fisheries Science Center, Narragansett, RI, 02882, USA

^b Anderson Cabot Center for Ocean Life, New England Aquarium, Boston, MA, 02110, USA

^c Biology Department, Dalhousie University, 1355 Oxford St, PO Box 15000, Halifax, NS, B3H4R2, Canada

^d Biology Department, Woods Hole Oceanographic Institution, 360 Woods Hole Road, Woods Hole, MA, 02540, USA

^e Northeast Fisheries Science Center, 166 Water St, Woods Hole, MA, 02543, USA

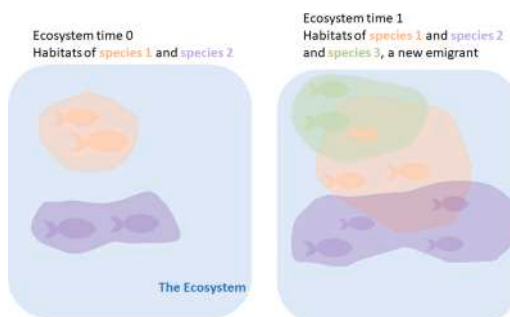
^f CASE Consultants International, 1 Haywood St Suite 451, Asheville, NC, 28801, USA

^g Gloucester Marine Station and Department of Environmental Conservation, University of Massachusetts Amherst, Holdsworth Hall, 160 Holdsworth Way, Amherst, MA, 01003, USA

HIGHLIGHTS

- Marine ecosystems are experiencing changes in species distribution and habitat.
- These changes may be affecting fish population abundance and biomass.
- Data for the Northeast US Shelf ecosystem suggests an increase in population sizes.
- These increases in population appear to be related to a decline in body size.
- Population and body size reorganization is consistent with system tropicalization.

GRAPHICAL ABSTRACT



With climate change, increased temperature can expand the habitats for species and open habitat for new species. The increased habitat areas can support larger populations. The larger populations and resulting competition has the effect of limiting growth.

ARTICLE INFO

Editor: Jay Gan

Keywords:

Biomass

Body size

Habitat

Climate change

Fisheries catch

Density dependence

Tropicalization

ABSTRACT

Climate change is profoundly affecting the physical environment and biota of the Northeast U.S. Continental Shelf ecosystem. To understand adaptations to climate change, in particular warming temperatures, we used bottom trawl survey data to describe the size of individual fish and macroinvertebrates. Using species distribution models to estimate abundance and biomass, we determined body size in weight for all modeled species. We demonstrate a tendency for increased abundance and biomass and a concomitant decline in body size over time. An analysis of length frequency data supports this assertion. There was no trend in the combined anthropogenic removals from the ecosystem, i.e. catches, suggesting a limited role of fisheries in influencing these changes. The changes in the fish and macroinvertebrate communities are consistent with the hypothesis of a tropicalization of this ecosystem, where the ecosystem experiences a change in diversity, abundance, biomass,

* Corresponding author.

E-mail address: kevin.friedland@noaa.gov (K.D. Friedland).

<https://doi.org/10.1016/j.scitotenv.2023.166117>

Received 25 May 2023; Received in revised form 4 August 2023; Accepted 5 August 2023

Available online 10 August 2023

0048-9697/Published by Elsevier B.V.

and the size of individuals consistent with lower latitudes. The changes in how productivity is expressed in the ecosystem factors into how human populations relate to it; in a practical sense, change in body size will likely influence the strategies and efficiencies of harvest procedures and the industries built to support them.

1. Introduction

Climate change is transforming marine ecosystems in myriad fashion including organismal and community level effects. Individuals experience changes to their basal metabolism (Carozza et al., 2019; Little et al., 2020), the quality and quantity of available food items (Boveng et al., 2020; Domenici et al., 2019), and the range of predation threats they must contend with to survive (Arimitsu et al., 2021; Goodman et al., 2022). Marine communities are likely to see change in their species diversity and evenness (Doney et al., 2012; Ibarbalz et al., 2019), the energy flow through different functional groups and trophic levels (Eddy et al., 2021), and changes to abundance and body size (Audzijonyte et al., 2020; Sheridan and Bickford, 2011). It is this latter issue that has caught our attention, especially in regard to changes that are occurring in middle latitude marine ecosystems, where species movement and replacement are occurring at a high rate (Hastings et al., 2020). Collectively, we can view these changes under the overarching descriptor of “tropicalization”, which is the transformation of temperate ecosystems by tropical organisms moving poleward in response to ocean warming (Osland et al., 2021). It is important to remember that tropicalization and deborealization are not mutually exclusive (McLean et al., 2021) in that the accumulation of warm water species does not necessarily have to be accompanied by the loss of boreal species.

The focus of our work is the Northeast U.S. Continental Shelf (NES) ecosystem, which is already demonstrating some aspects of tropicalization related to temperature change, species movement, and species richness. The NES ecosystem has warmed rapidly compared to other marine ecosystems worldwide (Saba et al., 2016). Temperature change has occurred in both the surface layer and in proximity to the benthos (Friedland et al., 2020b; Kavanaugh et al., 2017), in part due to the consequence of basin scale shifts in ocean circulation (Gonçalves Neto et al., 2021). Changes in the thermal environment (Thomas et al., 2017) have had subsequent biological effects, including species distributional ranges (Kleisner et al., 2017; Nye et al., 2009) and phenological relationships within the ecosystem (Staudinger et al., 2019). There has been an accumulated change in temperature that has exceeded 0.3 °C per decade over recent years and temperatures are expected to increase within this part of the North Atlantic through the end of the century (Grieve et al., 2017; Pershing et al., 2021; Saba et al., 2016). This multi-decadal warming pattern has reshaped NES biota in many ways. Most notably, there has been a general shift in distribution to higher latitudes and deeper depths among fish and macroinvertebrates (Record et al., 2019; Walsh et al., 2015). These shifts have not counteracted thermal exposure for fish and macroinvertebrate on the NES, which have an increasing community temperature index (CTI), especially in the autumn season (Friedland et al., 2019). Furthermore, distribution shifts have not been limited to upper trophic level organisms, but can be seen in the distribution of zooplankton as well (Friedland et al., 2019). Warming temperatures have transformed habitat, in some cases rendering it unsuitable for some resident species; as a consequence, local populations have become vulnerable to the potential of localized extirpation (Farr et al., 2021; Hare et al., 2016; Shackell et al., 2014). On the other hand, many taxa have expanded their range and habitat areas, perhaps mainly owing to a wider distribution of tolerable thermal conditions (Friedland et al., 2023). Collectively these changes have resulted in an increase in species richness for the NES (Batt et al., 2017) and likewise an increase in species diversity (Friedland et al., 2020a).

As an ecosystem with exploited species, there are a number of taxa in the NES that have been well studied and provide information related to changes in population size and the size of individuals. For example,

Atlantic haddock (*Melanogrammus aeglefinus*) has increased in abundance in recent years after a series of exceptional recruitment events (Friedland, 2021); and, coincidental with the change in population size, there has been a reduction in body size of haddock most likely due to intraspecific competition (Wang et al., 2021). The majority of commercially important finfish species assessed for fisheries management in the NES showed a decline in size at age in recent years (Friedland et al., 2020c). However, fishery independent surveys conducted in the NES capture many species that are not of commercial interest and are thus not assessed in any comprehensive fashion, although they are captured and often discarded in fisheries (Savoca et al., 2020). Attempts have been made to evaluate change in population size for all species captured in the NES as catch per unit effort, which suggested the expansion of fish and macroinvertebrate populations (Friedland et al., 2020a). More recently, the problem of estimating combined population size across species was approached through the use of habitat-informed stratified estimates of minimum population biomass, which also suggested an increase in biomass (Friedland et al., 2023). From these data, we can preliminarily conclude that fish and macroinvertebrate populations are expanding in the NES, while body size is declining. However, this conclusion is dependent on the extrapolation of trends from a small group of exploited taxa.

If the trends in population and body size can be confirmed more broadly, what is the underlying mechanism driving these changes? One hypothesis advanced is that with increasing temperature there is an expansion of habitat supporting endemic and newly established species (Friedland et al., 2020a). Hence, there is more habitat to accommodate increasing populations, which is accompanied by greater overlap between species habitats that results in greater interspecific competition. Competition then causes reduction of body size in individuals as food becomes limiting, compounded by the likelihood that food items are smaller and lower in energy content. This view is further complicated by indications that primary productivity has been declining in the NES (Balch et al., 2022). However, a fundamental underpinning of fisheries management is that fishing levels influence the abundance of stocks (Hilborn et al., 2020). Increasing fishing would be expected to diminish population size, and vice versa, with a decrease in fishing allowing for an expansion of populations. The effects of fishing can operate on varied spatial scales and may affect local abundances (Nillos Kleiven et al., 2019). Furthermore, fishing usually preferentially removes larger fish, which is driven by their higher market price (Tsikliras and Polymeros, 2014), creating a trend to smaller sized individuals, so fishing may affect body size in concert with or independently of the effects on population size (Haedrich and Barnes, 1997). It is also important to consider the role of selective harvest pressures on the genetics of fish populations, selecting for traits which include a conformation to smaller body size over a history of size selective removals (Swain et al., 2007).

An interest in population trajectory and body size is not limited to academic investigations, it clearly has societal ramifications with direct implications to resource utilization. The goal of fisheries management is the maintenance of yield through the control of spawning stock size and fishing rates, both of which are generally measured in biomass and thus mediated by abundances of all species and individual body sizes (Gaines et al., 2018; Hilborn et al., 2020). Fishing gears operate with some measure of size selectivity, thus an evolution of the size spectra of target and non-target species will undoubtedly affect the efficiency of fishery operations (Dean et al., 2021). A reduction of the size of target species will influence catchability and market appeal and greater catch of non-target species will increase the operational and regulatory burdens related to discards. Further, it is assumed in fisheries management that

egg production is proportional to the level of spawning stock biomass. However, we are seeing an increasing body of evidence that shows egg production can be quite variable, often related to the environment and competition affecting pre-spawning fish (Takasuka et al., 2019). Fishing communities will have to adapt to these sorts of changes by expanding the range of targeted species to match the evolving composition of fish and macroinvertebrates in the ecosystem, and will have to change and diversify their fishing gears and strategies to maintain productive catch levels (Young et al., 2019). In addition, fishery management systems will need to allow for this adaptation, with dynamic, adaptive approaches for climate-resilience (Holsman et al., 2019), or be re-designed to consider “planned adaptation” (Woods, 2022).

The purpose of this study was to determine whether there is additional evidence of tropicalization of the NES taking the form of a decline

in body size. The NES provides a unique opportunity to test this idea owing to the long-term monitoring programs that began six decades ago. The spatial coverage of these fishery independent bottom trawl surveys is from Cape Hatteras, North Carolina to Nova Scotia, Canada, with over 400 species identified in the survey (Friedland et al., 2020a). Though the intended purpose of the survey is to support fisheries management decision making, the data collected can be used to estimate species distribution and in turn abundance and biomass (Krebs et al., 1999). We used species distribution models to estimate abundance and biomass by species and infer change in body size both by individual taxa and collectively across the ecosystem. In addition, we tested the effects of fishing on body size by developing refined estimates of anthropogenic removals, recognizing this represents only a partial test of the phenomenon. We considered how changes in body size might affect human

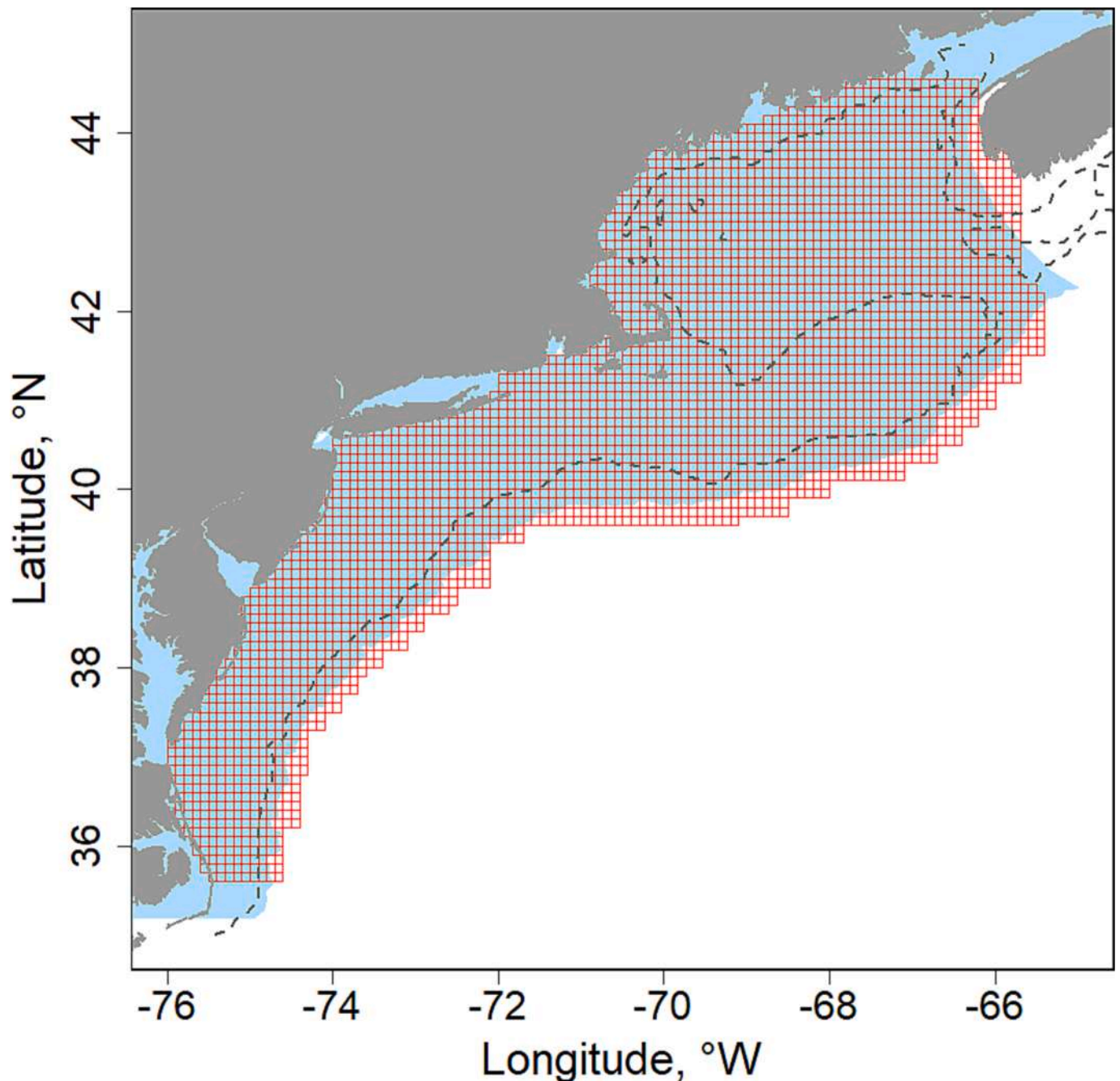


Fig. 1. Northeast US Continental Shelf with habitat area grid in red and extent of the Northeast US Continental Shelf large marine ecosystem in blue. Dashed line marks 100 m depth contour.

communities through the modification of fishing activities, and the ecosystem level effects of changes in size-specific relationships between taxa.

2. Methods

2.1. Study system, spatial frameworks, and temperature change context

This study focuses on the NES ecosystem, which has been demarcated by a number of spatial frameworks intended to help meet both scientific and management goals. We utilized two of these spatial frameworks to guide our data development. First, we used the grid that provided the basis to estimate habitat distribution in a series of models developed for NES species (Friedland et al., 2021b; Friedland et al., 2021a; Friedland et al., 2021c; Friedland et al., 2020a). The grid, which is shown in Fig. 1, is spaced by 0.1° increments and is intended to circumscribe a convention of ecoregion designations used in NES ecological studies (Lucey and Fogarty, 2013). We used this grid to estimate species abundance and biomass based on a swept area calculation, which is described in detail below. The second framework is the Northeast U.S. Continental Shelf large marine ecosystem designation, which is part of a global system of continental shelf seas ecosystems meant to represent global production units (Sherman and Duda, 1999); the extent of this large marine ecosystem is also shown in Fig. 1. The large marine ecosystem framework is used to estimate catch on a global scale, which we sourced from a community database (searounds.org) and adapted to the goals of this study, which is also described below.

Climate change context is provided by examining temperature trends over the study period. The study period of 1976–2019 exceeds the availability of remote sensing time series, thus representative surface and bottom temperature conditions were characterized from two observational data sources. Surface and bottom temperature over the NES for spring (April 3) and autumn (October 11) time frames were extracted from the gridded temperature products reported in Friedland et al. (2020b). This gridded data product is on the same grid shown in Fig. 1. Surface temperature data were also extracted from the NOAA Extended Reconstructed SST version 5 (Huang et al., 2017, p. 5); this dataset provides monthly temperature estimates, so for this analysis we extracted mean and range annually. Unlike the seasonal temperature data, the grid for this data product is relative course and spaced by 2° latitude and longitude increments; hence, eight grid locations were used to provide an SST index for the NES. We tested for time series trend in temperature with an auto-correlation corrected Mann-Kendall test (Yue et al., 2002) that also provided Theil–Sen slopes estimates (“zyp.trend.vector” command from R package zyp version 0.10–1.1; <https://cran.r-project.org/web/packages/zyp/>). This approach was used to test for trends in other study time series data.

2.2. Habitat inferred from species distribution models

We sought to provide estimates of abundance and biomass for most species occurring on the NES based on habitat distribution inferred from species distribution model output. The species distribution models used here are an extension of the model versions used most recently in Friedland et al. (2023). In that study, random forest classification models of presence/absence were used to estimate occurrence probability distributions; we take these distributions to represent occupancy habitat of the species. Random forest models were fit for a pool of species captured in the Northeast Fisheries Science Center bottom trawl survey (Desprespatanjo et al., 1988). This survey samples fish and macroinvertebrates in the NES during two seasonal time frames, spring and autumn, at a sample intensity of approximately 300 stations per season. The autumn bottom trawl survey began in 1963 and the spring survey began in 1968. Survey stations are located in continental shelf waters off the coast of North Carolina to Nova Scotia based on a stratified random sampling design. In addition to the total number and weight

of species, the survey logs trawl position, surface and bottom temperature, surface and bottom salinity, as well as information on individual organisms such as length and weight.

The presence or absence of a species was modeled based on a starting group of 91 explanatory variables. The initial group of variables was tested for collinearity and correlated variables were removed from the fitting procedure (“multi.collinear” command from R package rfUtilities version 2.1–5; <https://cran.r-project.org/web/packages/rfUtilities/index.html>). From the reduced set of variables, an optimal model was selected using the method described in Murphy et al. (2010), which determined the final set of variables included in a species model by successive model fitting (“rf.modelSel” command from R package rfUtilities). The candidate set of explanatory predictors included variables representing the physical oceanography, the distribution of lower trophic levels productivity (i.e., zooplankton as a measure of potential prey availability), and the benthic terrain of the ecosystem (see Supplementary Material for detailed listings of covariates). The training and testing dataset had a time series duration of 1976 to 2019 and was used to test model fits for 223 species, which included all species meeting the minimum criterion of having at least 50 occurrences in either the spring or autumn surveys. A species seasonal model was accepted if it had an area under the receiver-operator characteristic curve score or AUC (Fielding and Bell, 1997) of at least 0.7 resulting in satisfactory model fits for 177 species (Table 1). Of these satisfactory models, there were 121 species with spring models, 169 species with autumn models, and 113 species with models in both seasons. We have organized these taxa into two groupings including a common pool of species for those taxa common to both spring and autumn surveys, and taxa exclusive of the common pool. Additionally, the common pool species have no more than one year of missing data in a seasonal time series. There were 51 common pool species given the inclusion criteria, including the most common species captured in the survey and for which the survey was designed to target (Table 1). The balance of the species used in the study include 126 taxa that were modeled in one or both seasons and had varying numbers of years with missing data. We develop data for the common pool of species (51 taxa) and for all species up to 121 and 169 taxa in spring and autumn, respectively. So as a point of departure for the description of the calculation of abundance and biomass, each species represented by a seasonal model had estimates of yearly occurrence probability over the NES extent represented by the grid in Fig. 1 during the period 1976–2019.

2.3. Habitat informed estimates of abundance and biomass

To estimate the minimum population abundance and biomass of each species by season, we re-stratified the study area each year and season depending on the distribution of occupancy habitat (occurrence probability). The habitat was partitioned into ten strata based on the probability of occurrence from the species distribution model. The partitions were based on equal intervals of occurrence probability; hence, the size of each habitat strata could vary. The trawl catch-per-unit-effort (CPUE) values of either abundance or biomass were assigned to the appropriate habitat strata based on the habitat score of the location of the trawl haul. Tows from different vessels and gear configurations were standardized to a mean swept area of about 0.038 km² per tow (NEFSC Vessel Calibration Working Group, 2007) and reconciled with calibration factors applied to the total catch at each sampling station for each species (Miller et al., 2010). The calibration typically involved special cruise efforts where paired tows provided species-specific information on the factors in question, be it gear or vessel related. Once the requisite trawl hauls associated with a habitat stratum were identified, a mean CPUE was determined and raised to a total minimum population estimate for that stratum assuming a constant trawl path area of standard tow. The total population was the sum of the estimates for the ten strata.

Table 1

Species with distribution models and population estimates in one or both spring and autumn seasons (“s” spring season model, “a” autumn season model). Common pool species denoted in bold.

Species				
<i>Acanthocarpus alexandri</i>	s,a	<i>Glyptocephalus cynoglossus</i>	s,a	<i>Pandalus montagui</i>
<i>Acipenser oxyrinchus</i>	s	<i>Gymnura altavela</i>	a	<i>Paralichthys dentatus</i>
<i>Alosa aestivialis</i>	s,a	<i>Gymnura micrura</i>	a	<i>Paralichthys oblongus</i>
<i>Alosa pseudoharengus</i>	s,a	<i>Helicolenus dactylopterus</i>	s,a	<i>Parasudis triculenta</i>
<i>Alosa sapidissima</i>	a	<i>Hemirhamphus americanus</i>	s,a	<i>Pasiphaea multidentata</i>
<i>Amblyraja radiata</i>	s,a	<i>Hippoglossoides platessoides</i>	s,a	<i>Peprilus alepidotus</i>
<i>Ammodytes dubius</i>	s,a	<i>Hippoglossus hippoglossus</i>	s,a	<i>Peprilus triacanthus</i>
<i>Anarhichas lupus</i>	s,a	<i>Homarus americanus</i>	s,a	<i>Peristedion miniatum</i>
<i>Anchoa hepsetus</i>	a	<i>Illex illecebrosus</i>	s,a	<i>Placopecten magellanicus</i>
<i>Anchoa mitchilli</i>	s,a	<i>Lagodon rhomboides</i>	a	<i>Pogonias cromis</i>
<i>Antigonia capros</i>	s,a	<i>Larimus fasciatus</i>	a	<i>Pollachius virens</i>
<i>Argentina silus</i>	s,a	<i>Lebbeus polaris</i>	s,a	<i>Polymixia lowei</i>
<i>Argentina striata</i>	s,a	<i>Leiostomus xanthurus</i>	s,a	<i>Pomatomus saltatrix</i>
<i>Ariomma bondi</i>	a	<i>Lepophidium profundorum</i>	s,a	<i>Pontophilus norvegicus</i>
<i>Aspidophoroides monopterygius</i>	s,a	<i>Leucoraja erinacea</i>	s,a	<i>Prionotus alatus</i>
<i>Astroscopus guttatus</i>	a	<i>Leucoraja garmani</i>	s,a	<i>Prionotus carolinus</i>
<i>Bairdiella chrysoura</i>	a	<i>Leucoraja ocellata</i>	s,a	<i>Prionotus evolans</i>
<i>Balistes capriciscus</i>	a	<i>Limanda ferruginea</i>	s,a	<i>Pseudopleuronectes americanus</i>
<i>Bathynectes longispina</i>	s,a	<i>Limulus polyphemus</i>	s,a	<i>Rachycentron canadum</i>
<i>Bathypolypus arcticus</i>	s,a	<i>Liparis atlanticus</i>	s,a	<i>Raja eglanteria</i>
<i>Brevoortia tyrannus</i>	s,a	<i>Lithodes maja</i>	s,a	<i>Rhinoptera bonasus</i>
<i>Brosme brosme</i>	s,a	<i>Lolliguncula brevis</i>	a	<i>Rhizoprionodon terraenovae</i>
<i>Callinectes sapidus</i>	s,a	<i>Lophius americanus</i>	s,a	<i>Sardinella aurita</i>
<i>Cancer borealis</i>	s,a	<i>Lopholatilus chamaeleonticeps</i>	s,a	<i>Scomber colias</i>
<i>Cancer irroratus</i>	s,a	<i>Lumpenus lumpretaeformis</i>	s,a	<i>Scomber scombrus</i>
<i>Caranx crysos</i>	a	<i>Lumpenus maculatus</i>	s	<i>Scomberesox saurus</i>
<i>Caranx hippos</i>	a	<i>Macrorhamphosus scolopax</i>	s,a	<i>Scomberomorus cavalla</i>
<i>Carcharhinus obscurus</i>	a	<i>Macrozoarces americanus</i>	s,a	<i>Scomberomorus maculatus</i>
<i>Carcharhinus plumbeus</i>	a	<i>Majidae</i>	a	<i>Scophthalmus aquosus</i>
<i>Carcharias taurus</i>	a	<i>Malacoraja senta</i>	s,a	<i>Scyliorhinus retifer</i>
<i>Caretta caretta</i>	a	<i>Maurolicus weitzmani</i>	s,a	<i>Sebastes fasciatus</i>
<i>Centropristis striata</i>	s,a	<i>Melanogrammus aeglefinus</i>	s,a	<i>Selar crumenophthalmus</i>
<i>Chaetodipterus faber</i>	a	<i>Melanostigma atlanticum</i>	s,a	<i>Selene setapinnis</i>
<i>Chilomycterus schoepfi</i>	a	<i>Menidia menidia</i>	s	<i>Seriola zonata</i>
<i>Chionoecetes opilio</i>	s,a	<i>Menticirrhus americanus</i>	a	<i>Sicyonia brevirostris</i>
<i>Chlorophthalmus agassizi</i>	s,a	<i>Menticirrhus saxatilis</i>	a	<i>Spherooides maculatus</i>
<i>Citharichthys arctifrons</i>	s,a	<i>Merluccius albidus</i>	s,a	<i>Sphyræna borealis</i>
<i>Clupea harengus</i>	s,a	<i>Merluccius bilinearis</i>	s,a	<i>Spirontocaris lijeborgii</i>
<i>Conger oceanicus</i>	s,a	<i>Micropogonias undulatus</i>	s,a	<i>Squalus acanthias</i>
<i>Crangon septemspinosa</i>	s,a	<i>Monacanthus hispidus</i>	a	<i>Squatina dumeril</i>
<i>Cryptacanthodes maculatus</i>	s,a	<i>Monolene sessilicauda</i>	s,a	<i>Stenotomus caprinus</i>
<i>Cyclopterus lumpus</i>	s,a	<i>Morone saxatilis</i>	s,a	<i>Stenotomus chrysops</i>
<i>Cynoscion nothus</i>	a	<i>Mullus auratus</i>	a	<i>Stoloteuthis leucoptera</i>
<i>Cynoscion regalis</i>	s,a	<i>Mustelus canis</i>	s,a	<i>Symphurus plagiosa</i>
<i>Dasyatis americana</i>	a	<i>Myliobatis freminvillei</i>	a	<i>Synagrops bellus</i>
<i>Dasyatis centroura</i>	a	<i>Myoxocephalus aeneus</i>	s,a	<i>Syngnathus fuscus</i>
<i>Dasyatis say</i>	a	<i>Myoxocephalus octodecemspinus</i>	s,a	<i>Synodus foetens</i>
<i>Decapterus macarellus</i>	a	<i>Myxine glutinosa</i>	s,a	<i>Tautoga onitis</i>
<i>Decapterus punctatus</i>	a	<i>Nemichthys scolopaceus</i>	a	<i>Tautoglabrus adpersus</i>
<i>Dichelopandalus leptocerus</i>	s,a	<i>Nezumia bairdi</i>	s	<i>Torpedo nobilitiana</i>
<i>Dipturus laevis</i>	s,a	<i>Octopus vulgaris</i>	s,a	<i>Trachurus lathami</i>
<i>Doryteuthis pealeii</i>	s,a	<i>Ophidion grayi</i>	a	<i>Trichiurus lepturus</i>
<i>Enchelyopus cimbrius</i>	s,a	<i>Ophidion marginatum</i>	s,a	<i>Triglops murrayi</i>
<i>Engraulis eurystole</i>	a	<i>Opisthonema oglinum</i>	a	<i>Trinectes maculatus</i>
<i>Etropus microstomus</i>	s,a	<i>Orthopristis chrysoptera</i>	a	<i>Urophycis chesteri</i>
<i>Etrumeus teres</i>	a	<i>Osmerus mordax</i>	s	<i>Urophycis chuss</i>
<i>Foetorepus agassizi</i>	s,a	<i>Ovalipes ocellatus</i>	s,a	<i>Urophycis regia</i>
<i>Gadus morhua</i>	s,a	<i>Ovalipes stephensoni</i>	s,a	<i>Urophycis tenuis</i>
<i>Geryon quinquegens</i>	s,a	<i>Pandalus borealis</i>	s,a	<i>Zenopsis conchifera</i>

$$\text{Total abundance or biomass} = \sum_{i=1}^{10} \frac{\text{strata area}}{\text{trawl path area}} \times \text{mean CPUE}$$

These estimates were conditioned by interpolating over habitat strata by applying a smoother across the mean CPUE estimates in each stratum. A loess smoother (span = 0.75) was applied to generate the smoothed catch rates; the procedure also had the benefit of interpolating and extrapolating a rate to a habitat stratum that may not have had catch samples associated with it. Estimates of aggregate abundance and biomass across all species and across all common pool species were obtained by summing the estimates over the individual species. The

biomass associated with the species that had habitat models accounted for on average 98 % and 99 % of the total biomass sampled by the trawl survey in spring and autumn, respectively. We tested for time series trends in abundance and biomass in aggregate for common pool and all species, and for individual species.

2.4. Indicators of body size

We considered body size as either weight or length of an individual. The weight of individuals was calculated as the biomass divided by the associated abundance by species and year. Missing values were excluded

from the analysis. As a composite signal, the median of species' weights was determined each year. As done for the abundance and biomass time series data, a trend statistic was calculated for the composite signals (common pool and all species) and the trend was evaluated for each species, noting the number of positive and negative trends among those species with significant trends. A different approach was taken with the length data. The abundance of each species is assigned to length (cm) within each tow. We determined the mean length of each species by year by combining the length frequency data across tows. The composite length signal was computed as the median across species excluding missing values. Seven taxa, all of which were shrimp species, had no associated length data. Similar to the treatment of abundance and biomass mentioned above, we tested for time series trend in weight and length in aggregate for common pool and all species, and for individual species. Because of the rigor of our statistical trend test, we anticipated modest numbers of individual species trend tests for these four data types would be significant at the conventional probability of 0.05. Hence, we also collected data on the trend tests at a relaxed probability of 0.1 to increase the grouping size of trends to compare.

2.5. Anthropogenic removals from the ecosystem

Recognizing that anthropogenic removals can influence patterns of species abundance and biomass, an estimate of fisheries catches associated with the study domain was adapted from a global data product. The Sea Around Us project database provides estimates of reconstructed catch in the Northeast U.S. Continental Shelf large marine ecosystem that includes landings, discards, and unreported catches (Zeller et al., 2016). Catches in this database are coded by common and scientific names and contain designations of scientific names that matched the listing of putative estuarine species in Table 2. These estuarine species were excluded from the analysis since they are considered to be mostly distributed and harvested in estuarine waters and thus outside the study grid. This listing contains the most important contributors of estuarine catch including *Brevoortia tyrannus*, *Callinectes sapidus*, and *Crassostrea virginica*, but it is not exhaustive of all species captured in estuaries. It is limited to taxonomic designations that could be matched to designations in the database. We could not clearly account for designations for some species in the catch data, such as *Mya arenaria*, that was likely contained in a broader designation in the catch data such as clams. However, since we are accounting for the main catch contributors from estuaries, we feel that the exclusions are adequate to make the catch time series mostly indicative of removals that correlate to our study grid. Trend statistics were calculated for the combined common pool and all species time series. The relationship between catch and either abundance or biomass was evaluated with Spearman rank correlation. As applied to the trend statistic, the correlation tests were corrected for serial correlation using the methods of Lun et al. (2022). We used the significance test of rank cross-correlation from the "corTESTsrd" R package (version

Table 2

Estuarine taxa, including both species and family names as used in the database, excluded from the catch time series. Percent contribution of the catch to the total removed from the Sea Around Us database.

Scientific Name	Percent	Scientific Name	Percent
<i>Brevoortia tyrannus</i>	59.6	<i>Strongylocentrotus droebachiensis</i>	0.1
<i>Crassostrea virginica</i>	19.2	<i>Ensis directus</i>	0.1
<i>Callinectes sapidus</i>	10.4	<i>Cyprinus carpio</i>	0.1
<i>Morone saxatilis</i>	4.5	<i>Buccinum undatum</i>	<0.1
<i>Micropogonias undulatus</i>	2.1	<i>Strongylocentrotus</i>	<0.1
<i>Argopecten irradians</i>	1.1	<i>Menidia menidia</i>	<0.1
<i>Leiostomus xanthurus</i>	1	<i>Alosa mediocris</i>	<0.1
Brachyura	0.7	<i>Carcinus maenas</i>	<0.1
<i>Morone americana</i>	0.5	Mugilidae	<0.1
<i>Anguilla rostrata</i>	0.2	Cyprinidae	<0.1
<i>Alosa sapidissima</i>	0.2	<i>Anchoa mitchilli</i>	<0.1
<i>Dorosoma cepedianum</i>	0.1		

1.0–0). All correlation tests were reported with adjusted *p*-values. Correlations were calculated for the combined catch and abundance or biomass and for those individual species that could be identified in the database, grouped by those within the common pool of species and all study species. In both instances, for total catch and catch by species, the presence of a negative correlation with abundance or biomass would be an indication of the potential of fisheries effects; a decline in catch would allow species abundance and biomass to increase, and vice versa, an increase in catch would lower abundance and biomass. A positive correlation would indicate catch was following population size expressed as abundance or biomass, where change would more likely be related to environmental effects. For combined catch correlations, we also tested the effects of three time lags (catch at 1–3 years prior to the abundance and biomass estimates) under the assumption that catch may have a delayed effect on abundance and biomass.

3. Results

3.1. Change in the thermal conditions of the NES

The temperature conditions in both surface and bottom waters of the NES have changed over the study period. Spring surface water temperatures tended to run slightly lower than spring bottom temperature and lacked a time series trend compared to the bottom temperature (Fig. 2a, b). The trend in spring bottom temperature was 0.30 °C decade⁻¹. Autumn surface and bottom water temperatures both trended significantly with rates of change of 0.48 and 0.39 °C decade⁻¹, respectively (Fig. 2c,d). The annual mean for the system trended at a rate of 0.29 °C decade⁻¹ owing in large measure to the increasing trend in temperature range of 0.38 °C decade⁻¹, reflecting the seasonal differences in warming rates seen in the spring and autumn data (Fig. 2e,f).

3.2. Habitat informed trends in abundance and biomass

Between 1976 and 2019 composite abundance and biomass increased in both spring and autumn seasons. This composite increase was supported by the increasing trends for abundance and biomass among contributing individual species. The composite abundance of all modeled species in the spring was approximately 3.6×10^9 individuals at the beginning of the time series and increased to approximately 6.8×10^9 individuals at the end of the series (Fig. 3a). The composite abundance of common pool species followed a similar trend and the mean difference was approximately 1.3×10^9 less individuals each year that for the all species (Fig. 3b). The trends for these composite time series were both significant (Table 3). The trends among individual species were mostly positive. Of the 121 modeled species, 48 (40 %) had significant trends in spring abundance, 77 % of which were positive trends (Table 4). In a similar manner, the trends among common pool individual species were mostly positive. Of the 51 modeled species, 23 (45 %) had significant trends in spring abundance, 74 % of which were positive trends (Table 4). For this first case comparison, the trends among species conditioned by a probability cutoff of $p = 0.05$ were mirrored by the data conditioned with a cutoff $p = 0.1$; these tests have the benefit of comparisons made on a larger sample sizes of significant trends. This is generally true for the balance of the species trends tests, so the comparison will not be explicitly mentioned again.

Spring composite biomass for all and common pool species both increased significantly (Fig. 3c&d). Moreover, the percentage of species with increasing trends in biomass were 68 and 56 % for composite and common pool species, respectively. In autumn, the composite estimates of abundance and biomass for all and common pool species increased significantly (Fig. 4a-d). The trends in abundance among all individual species changed significantly in 64 taxa, and 78 % of which were positive trends; among common pool species, 28 taxa had significant trends, and 64 % were positive. Similarly, 59 of all species had significant trends, and 76 % of which were positive; among common pool species,

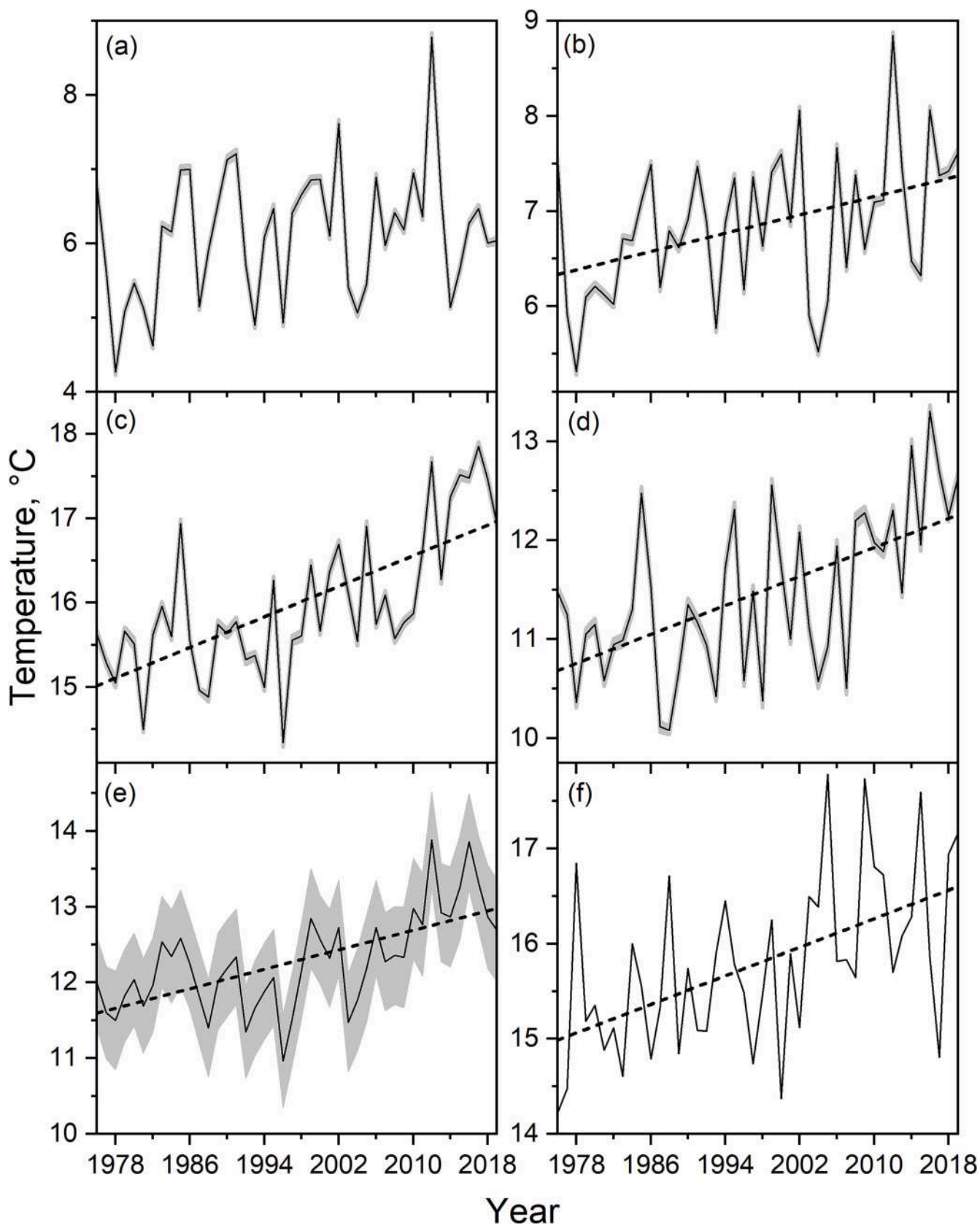


Fig. 2. Water temperature in the NES. Spring surface (a), spring bottom (b), autumn surface (c), and autumn bottom (d) temperature based on in situ interpolation temperature data. Mean (e) and range (f) of surface temperature from the ERSST dataset. Dashed lines are linear regressions associated with significant trends; gray shading represents the standard error of the mean where appropriate.

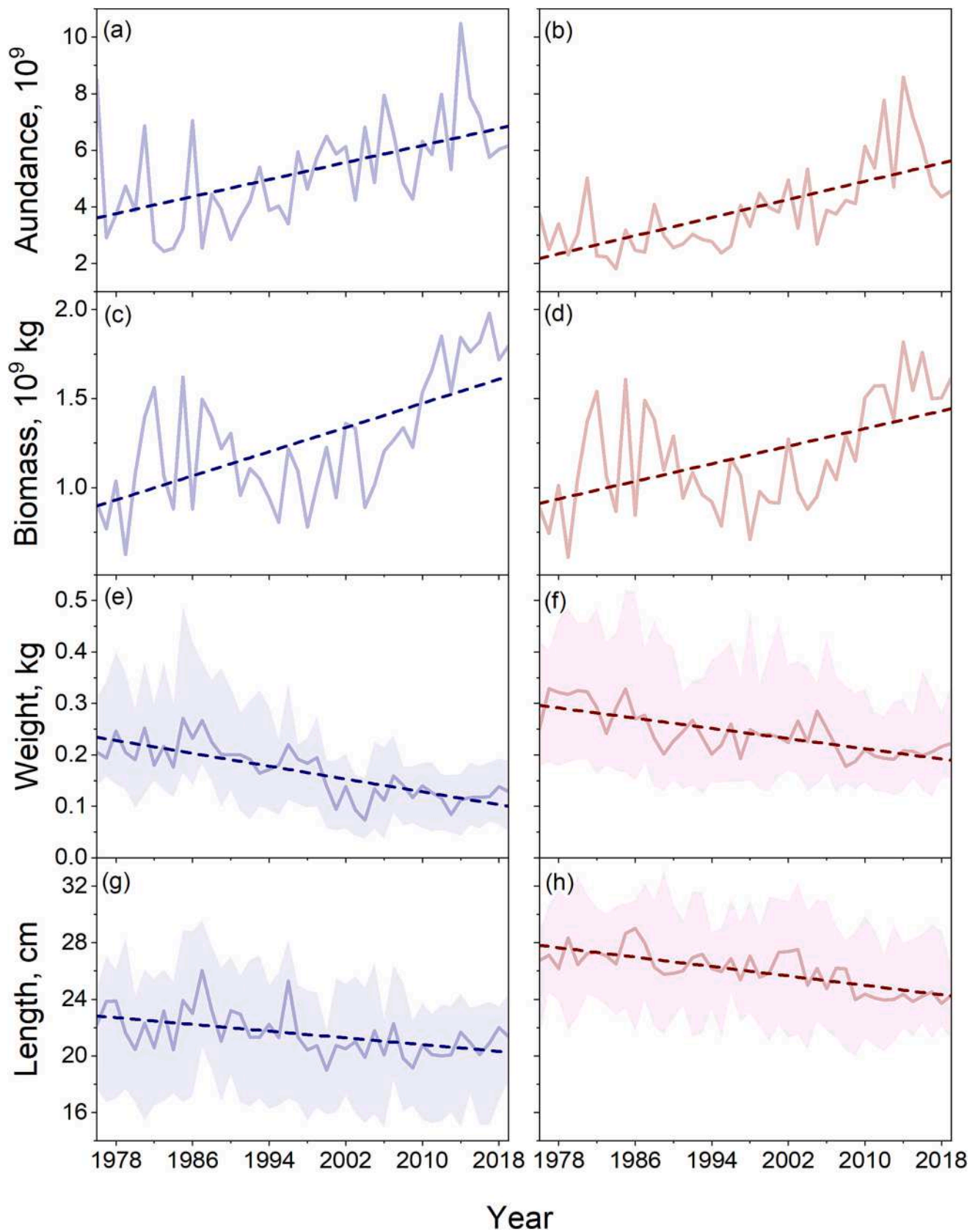


Fig. 3. Time series trends in abundance, biomass, weight and length for all species (panels a, c, e, and g, respectively) and common pool species (panels b, d, r, and h, respectively) during spring. Dashed lines are linear regressions associated with significant trends; shading represents the 95 % confidence interval of the median where appropriate.

Table 3

Trend (as Theil–Sen slope estimators) of combined abundance and biomass of all taxa and median weight and length of individuals for all species. Mann-Kendall Trend Test probability (p) and the number of taxa included in each test (N) for all species and the common species group. Statistical significance denoted with bold.

Group	Season	Parameter	Unit	Trend	p	N
All	Spring	Abundance	Number	87,175,119	0.000	121
		Biomass	kg	18,395,190	0.002	121
		Weight	kg	-0.0030	0.000	121
		Length	cm	-0.0568	0.003	114
	Autumn	Abundance	Number	116,027,822	0.021	169
		Biomass	kg	13,242,520	0.001	169
		Weight	kg	-0.0024	0.000	169
		Length	cm	-0.0133	0.586	162
Common	Spring	Abundance	Number	70,815,172	0.000	51
		Biomass	kg	13,137,341	0.005	51
		Weight	kg	-0.0026	0.000	51
		Length	cm	-0.0806	0.000	51
	Autumn	Abundance	Number	121,363,456	0.000	51
		Biomass	kg	11,520,298	0.003	51
		Weight	kg	-0.0027	0.012	51
		Length	cm	-0.0756	0.002	51

Table 4

The number of species-specific significant Mann-Kendall Trend Tests of abundance, biomass, weight, and length with probabilities $p < 0.1$ and 0.05 for all taxa (N) for all species and the common species group. Percent negative and positive refers to the percentage of total significant tests.

Group	Season	Parameter	Number	Number	Total	Percent	Percent	N	
			Negative	Positive		Negative	Positive		
			0.1, 0.05	0.1, 0.05	0.1, 0.05	0.1, 0.05	0.1, 0.05		
All	Spring	Abundance	15, 11	48, 37	63, 48	24, 23	74, 77	121	
		Biomass	18, 18	44, 38	62, 56	29, 32	71, 68	121	
		Weight	35, 32	10, 10	45, 42	78, 76	22, 24	121	
		Length	31, 25	13, 9	44, 34	70, 74	29, 26	114	
	Fall	Abundance	19, 14	62, 50	81, 64	23, 22	77, 78	169	
		Biomass	19, 14	56, 45	75, 59	25, 24	75, 76	169	
		Weight	39, 30	13, 10	52, 40	75, 75	25, 25	169	
		Length	29, 25	22, 18	51, 43	57, 58	43, 42	162	
Common	Spring	Abundance	8, 6	19, 17	27, 23	30, 26	70, 74	51	
		Biomass	11, 11	17, 14	28, 25	39, 44	61, 56	51	
		Weight	26, 25	6, 6	32, 31	81, 81	19, 19	51	
		Length	23, 21	6, 4	29, 25	79, 84	21, 16	51	
	Fall	Abundance	12, 10	23, 18	35, 28	34, 36	66, 64	51	
		Biomass	12, 9	21, 18	33, 27	36, 33	64, 67	51	
		Weight	22, 16	5, 5	27, 21	81, 76	19, 24	51	
		Length	16, 13	7, 7	23, 20	70, 65	30, 35	51	

27 had significant trends, and 67 % of which were positive. In summary, for both all and common pool species groups, both abundance and biomass increased over the study period as evidenced by the trends in composite data and among trends for individual species.

3.3. Trends in the size of individuals

There are indications that the size of individual fish and macro-invertebrates have decreased in composite estimates and for individual taxa over the time series. The composite median individual weight (hereafter, weight) of all species in the spring was approximately 0.23 kg at the beginning of the time series and declined to approximately 0.10 kg at the end of the series (Fig. 3e). The composite weight of common pool species followed a similar trend and averaged approximately 0.08 kg lighter than the all species median (Fig. 3f). The trends for the composite time series were both significant (Table 3). The trends among individual species were mostly negative. Of the 121 modeled species, 42 (35 %) had significant trends in spring weight, 76 % of which were negative trends (Table 4). Following, the trends among common pool individual species were mostly negative. Of the 51 modeled species, 31 (61 %) had significant trends in spring weight, 81 % of which were negative trends (Table 4).

Spring length for the composite and common pool species both decreased significantly (Fig. 3g&h). In addition, the percentage of species with decreasing trends in length were 74 and 84 % for all and

common pool species, respectively. In autumn, the composite estimates of weight for all and common pool species decreased significantly (Fig. 4e&f). However, only the common pool length composite signal was found to be significant, whereas the all-species signal was non-significant (Fig. 4g&h). The trends in weight among all species changed significantly in 40 taxa, and 75 % of which were negative trends; and, among common pool species, 21 taxa had significant trends, and 76 % were positive. Similarly, 43 of all species had significant length trends, and 58 % of which were positive; and, 20 common pool species had significant trends, and 65 % of which were negative. In summary, for both all and common pool species groups, both weight and length declined during spring over the study period time series. However, during autumn, though there were strong indicators of a decline in weight, the trends in length were mixed.

3.4. Anthropogenic removals from the ecosystem

Catch in the NES ecosystem showed decadal variability but lacked any long-term trend. Catches for those species that could be identified as part of the common pool averaged approximately $760,000 \text{ mt y}^{-1}$ and lacked any trend ($p = 0.98$) over the study period (Fig. 5a). Similarly, the catches for all species excluding those considered to be estuarine averaged approximately $1.3 \times 10^6 \text{ mt y}^{-1}$ and also lacked any trend ($p = 0.22$) over the study period (Fig. 5b). Any potential relationship between catch and abundance or biomass was tested with Spearman correlation;

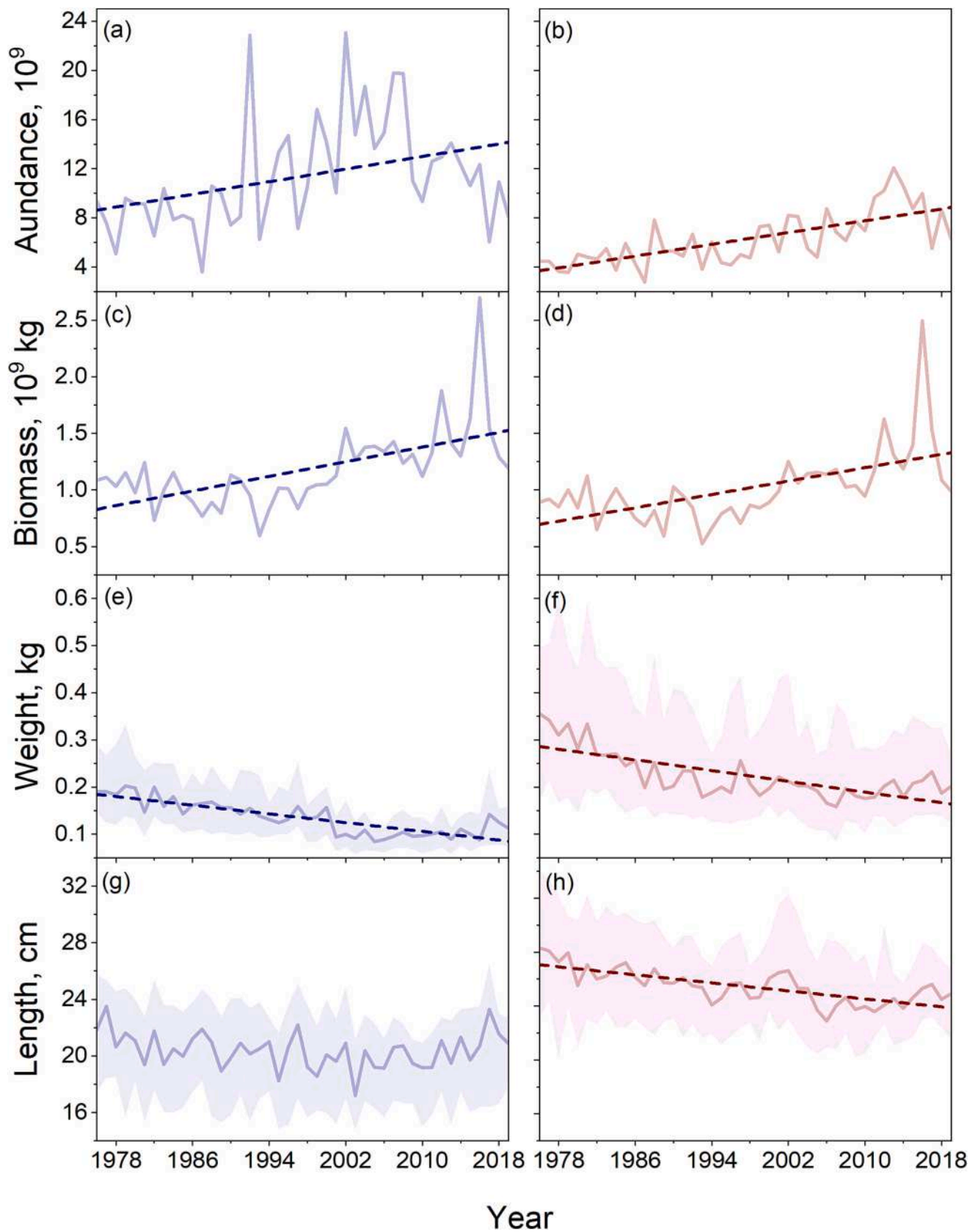


Fig. 4. Time series trends in abundance, biomass, weight and length for all species (panels a, c, e, and g, respectively) and common pool species (panels b, d, f, and h, respectively) during autumn. Dashed lines are linear regressions associated with significant trends; shading represents the 95 % confidence interval of the median where appropriate.

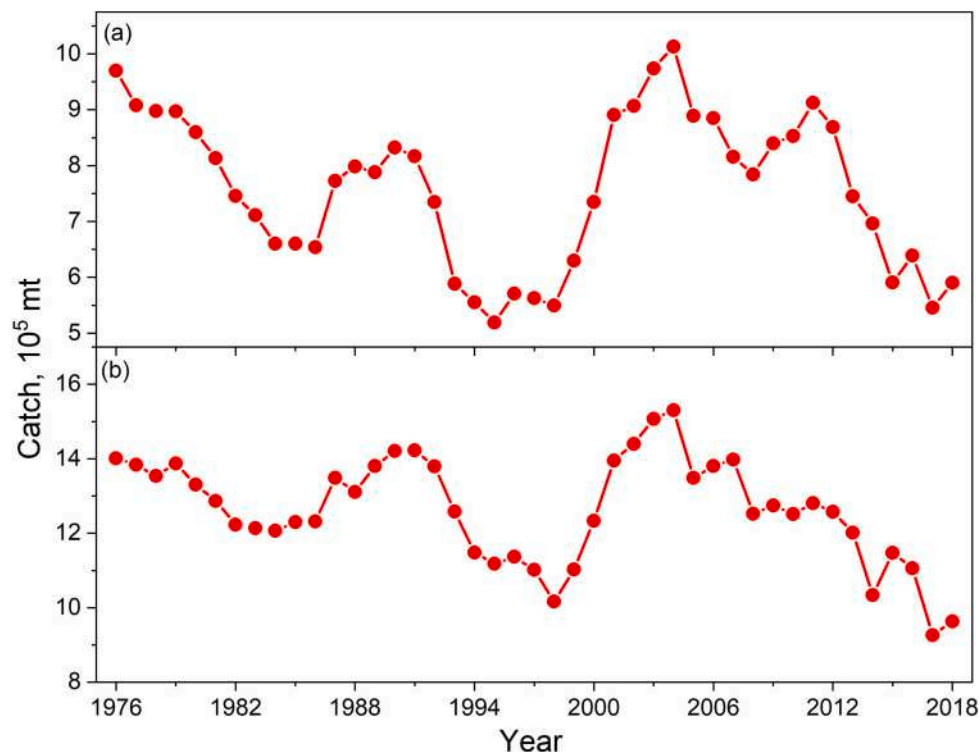


Fig. 5. Time series of catch estimates for common pool species that could be identified (a) and all taxa (b) in the Northeast US Continental Shelf large marine ecosystem based on the Sea Around Us database. Catch estimates are exclusive of the estuarine species listed in Table 3.

no significant correlations were found between either of these catch series and the related measures of abundance and biomass (Table 5). Furthermore, correlation at lags of 1 to 3 years also resulted in no significant correlations (the lowest p -values among these correlations was 0.232). Correlations between catch and abundance and biomass for individual species provided a more distinct pattern. For the 34 species in the common pool, correlations between catch and abundance and biomass tended to be mostly positive (Table 6). For example, 74 % of species-specific significant correlations between spring common pool abundance and catch were positive. Likewise, spring abundance and catch correlations among all species were mostly positive, as were correlations between biomass and catch for both species groupings. In the autumn data, the majority of the correlations were also positive, noting that the correlations between abundance and catch were the lowest of positive proportions at 65 %. With the exception of spring biomass correlations, which resulted in 14–15 significant correlations, the number of significant correlations were low, but were mostly positive in sign. In summary, catch estimates combined across all and among common pool species would suggest fishing activity plays a minor role in shaping the resultant patterns of abundance and biomass at the ecosystem scale. However, for a relatively small subgroup of species identified in the data, the predominance of positive correlations

between catch and abundance and biomass suggests an independence from fishing effects. These data suggest that catches scale with abundance and biomass and are more likely shaped by environmental factors.

3.5. Relationships between abundance, biomass, and thermal conditions

Abundance and biomass was positively correlated to change in thermal conditions on the NES. The sign of all correlations was positive and the strongest correlative density was concentrated in the mean annual temperatures and in autumn bottom temperatures (Table 7). Mean annual temperature and autumn bottom temperature were significantly correlated with three of the four abundance and biomass measures, the only non-significant tests were with autumn abundance. Autumn surface temperature was significantly correlated with spring and autumn biomass; and, spring bottom temperature was significantly correlated with spring abundance.

4. Discussion

A reduction in body size of fish and macroinvertebrates was observed in the NES ecosystem at both the community and individual species levels. Our working hypothesis, first suggested in Friedland et al. (2020a), is that thermal change in the ecosystem has expanded fish and macroinvertebrates habitat areas within the ecosystem allowing for expansion of extant populations. This expansion is occurring within the unchanging spatial confines of the ecosystem, resulting in greater competition between individuals (Friedland et al., 2020a). By extension, the size spectrum of prey utilized by predators would also have shifted to smaller, less energetic food items (Griffiths, 2020). We assume we are seeing the effects of competition combined with other factors like the physiological response of growth and body size to warming processes (Rindorf et al., 2022; Verberk et al., 2021), the result being the current disposition of the NES as a system with greater biomass among more numerous, smaller individuals. The abundance and biomass of all survey taxa in the NES, which includes many species not recorded as fisheries

Table 5
Spearman rank correlation between ecosystem catch estimates and abundance and biomass by season and species group.

Season	Group	Parameter	Spearman	p
Spring	All	Abundance	-0.064	0.749
		Biomass	-0.270	0.232
	Common	Abundance	0.103	0.675
		Biomass	-0.110	0.627
Autumn	All	Abundance	0.092	0.661
		Biomass	0.072	0.776
	Common	Abundance	0.059	0.809
		Biomass	0.300	0.250

Table 6

The number of species-specific Spearman rank correlations by sign and significance ($p < 0.05$) between catch and abundance and biomass for common pool and all species. The number of species with available data for each group shown as N. Percent negative and positive refers to the percentage of total tests.

Season	Parameter	Group	Number		Significant		N
			Negative	Positive	Negative	Positive	
Spring	Abundance	Common	9 (26)	25 (74)	1 (3)	6 (18)	34
		All	13 (31)	29 (69)	2 (5)	6 (14)	42
	Biomass	Common	7 (21)	27 (79)	0 (0)	14 (41)	34
		All	10 (24)	32 (76)	1 (2)	15 (36)	42
Autumn	Abundance	Common	12 (35)	22 (65)	1 (3)	4 (12)	34
		All	16 (29)	39 (71)	2 (4)	6 (11)	55
	Biomass	Common	10 (29)	24 (71)	1 (3)	6 (18)	34
		All	15 (27)	40 (73)	1 (2)	8 (15)	55

Table 7

Spearman rank correlation between abundance and biomass by season and thermal indicators by season. Significant p-values shown in bold.

Thermal Indicator	Season	Parameter	Spearman	p
Spring Surface	Spring	Abundance	0.196	0.202
		Biomass	0.070	0.665
	Autumn	Abundance	0.133	0.395
		Biomass	0.150	0.362
Spring Bottom	Spring	Abundance	0.410	0.011
		Biomass	0.270	0.103
	Autumn	Abundance	0.221	0.172
		Biomass	0.249	0.149
Autumn Surface	Spring	Abundance	0.393	0.054
		Biomass	0.502	0.024
	Autumn	Abundance	0.263	0.223
		Biomass	0.636	0.011
Autumn Bottom	Spring	Abundance	0.385	0.038
		Biomass	0.420	0.033
	Autumn	Abundance	0.158	0.410
		Biomass	0.435	0.046
Mean	Spring	Abundance	0.439	0.037
		Biomass	0.525	0.023
	Autumn	Abundance	0.187	0.399
		Biomass	0.613	0.021
Range	Spring	Abundance	0.138	0.428
		Biomass	0.237	0.186
	Autumn	Abundance	0.212	0.237
		Biomass	0.359	0.067

catch, has increased significantly despite an absence of trend in anthropogenic removals. This increase serves as a reminder that perception about biomass in marine ecosystems can only be partially explained by fisheries catch times series (Cheung et al., 2021; Pauly et al., 2013). Many species contributing to the NES community abundance and biomass are not landed since they are not generally accepted as food fish, often because they are recent additions to the fish community (Link, 2007). Hence, there is no established cultural tradition to market the fish and there is unlikely to be any shore side infrastructure to support their utilization (Hollowed et al., 2013; Weatherdon et al., 2016).

Observed declines in body size have been reported across many ecosystems globally, including in New Zealand (Lavin et al., 2022b), Norway (Lavin et al., 2022a), the North Sea (Baudron et al., 2014; Ikpewe et al., 2021), and broadly across Northwest Atlantic large marine ecosystems (Fisher et al., 2010). A foundational mechanism for body size change in a warming climate is based on the physiological response of fishes to increased temperature and oxygen stress (Cheung et al., 2013). In what has been termed the temperature–size rule, ectotherms grow to smaller sizes when they develop under higher temperatures. The size rule can be supported by the growth response of fish over temperature gradients in the Mediterranean Sea (van Rijn et al., 2017). However, when the rule was considered for coral reef fishes, the results were less clear and compounded by the spatial complexity of the study

ecosystem (Audzijonyte et al., 2020). Studies have shown heterogeneity in the magnitude and direction of size responses to climate effects, suggesting a need for large-scale comparative analyses (Gardner et al., 2011); but perhaps also supporting the idea that there are competing factors controlling body size. Fishing pressure is another driver of shrinkage that may act additively or even synergistically with warming, as evidenced for menhaden in the US Atlantic and Gulf of Mexico, from Maine to Texas (Turner, 2017). There are few empirical descriptions of the change in body size at the community level and almost a singular view of change in body size is dependent on physiological adaptation with temperature (Gårdmark and Huss, 2020). If the change in individual size was purely a response to changing temperature, it does not explain the concomitant change in population biomass. More recently, a hypothesis that narrows focus on oxygen limitation in warming waters as a mechanism to explain decreased body size in aquatic ectotherms has emerged (Pauly, 2021). Lindmark et al. (2022) found support for this theory using a meta-analysis of experimental studies that predicted a decline in optimum growth temperatures with body size. Overall, these studies suggest that declines in body size are widespread and often system dependent (Huang et al., 2021), although the mechanism is not fully understood, are coincident, suggesting a broad and ubiquitous driver.

In light of these arguments and experience elsewhere, anticipated future climate change in the NES, which we expect to continue current trends, will likely cause a further reduction of body size in the ecosystem. As developed in the introduction, the NES has seen climate change effects that are among the most pronounced worldwide and climate projection models predict further change to the NES climate system, in particular, continued warming. Change in body size has been noted as an important ecosystem response to climate change in US waters and in the NES specifically (Weiskopf et al., 2020). On a species level, we have seen growth and maturation responses in invertebrate species like *Homarus americanus* (Le Bris et al., 2017) and commercial fish taxa such as cod *Gadus morhua* (Pershing et al., 2016), both of which are key NES resource species. By considering the more comprehensive grouping of taxa from the bottom trawl survey, which included both lobster and cod as survey species, we can look beyond what is occurring to these species in isolation and more fully consider the changes in the ecosystem. Hence, past becomes prologue, and we see little evidence to fashion an argument that the fish and macroinvertebrate communities of the NES will not continue to expand and individual size continue to contract.

The increase in fish and macroinvertebrate abundance and biomass challenges the perception of a scaling between primary and secondary production in marine ecosystems. It has been expressed in a number of different ways, but a basic tenet in systems ecology is the idea that fish production is a function of phytoplankton primary production (Chassot et al., 2010). In some instances, chlorophyll biomass may be a responsive indicator of potential secondary fishery production owing to the energy pathways within an ecosystem (Friedland et al., 2012; Stock et al., 2017). Fisheries landings and catch, as noted, can sometimes be a poor indicator of system biomass, depending upon the desirability of

different taxa for harvest (Cheung et al., 2021; Pauly et al., 2013). In the NES, however, a relatively flat trajectory of fisheries catch exists with an underlying increasing trend in the biomass of secondary producers. The NES, like other continental shelf seas, has not experienced a contemporary increase in primary production (Friedland et al., 2020c). This perception is mainly built from remote sensing chlorophyll concentration data, but is also shown by in situ observations within the NES (Balch et al., 2022). This leaves a paradox of how an expansion of secondary production is possible with a decline in primary production. A hypothesis explored previously, and supported more formally here, is the idea that the fish and macroinvertebrate populations sampled by the trawl survey only intercept a portion of the primary production of the NES, the balance of which is being exported from the system (Friedland et al., 2020a). The export is achieved via sedimentation of fixed carbon, which joins fluidized sediments flowing off the shelf-break and into deeper water. Hence, with climate change there is a forced expansion of habitats for NES fish and macroinvertebrates species, facilitating larger populations that are scaling with habitat, leading to a greater fraction of the primary production being intercepted before it is sequestered. We recognize that our data cannot fully test this hypothesis, but believe it to be a worthwhile concept for additional research.

Energy and nutrient flows through the system are impacted by species abundance and it is possible that current productivity and ecosystem functioning have been diminished due to habitat loss and historical fisheries removals (Dias et al., 2019). Removals have occurred at all trophic levels (Lotze and Milewski, 2004) and changes occurred from megafauna to forage species, and the habitats that they associate with. As species are diminished, there can be loss of important conduits of energy through the system with the Gulf of Maine limited in the number of mid-trophic forage fish species (Dias et al., 2019). Further climate-induced impacts such as mismatches among trophic levels due to phenology shifts (Staudinger et al., 2019) may all contribute to changes in the ratio of system primary and secondary production. Yet, with these caveats, the period analyzed (1976–2019) demonstrated a relatively consistent trend towards smaller individuals, although the rate of change varied throughout the study period. It is also important to acknowledge that, while anthropogenic removals were relatively flat over the study period, the composition of fisheries catches was changing in response to abundance and constraining stocks. Catches of groundfish declined by half in the period of 1992–1999, and further again such that by 2015, Gulf of Maine and Georges Bank stocks of cod were constraining other groundfish catch like haddock (Scheld and Walden, 2018). While there was an expectation of an effect from anthropogenic removals on biomass, this was unsupported over the study period. Biomass increased under a regime of relatively constant catch, and under declining, or at best, unchanged primary production, which leaves only a limited range of possible drivers of community change.

A main limitation associated in using surveys to represent changing species abundance of differing functional groups is the varying levels of gear catchability. The survey gear used in this analysis targets groundfish species and must be considered a by-catch gear for most pelagic taxa (Desprespatanjo et al., 1988). Conclusions concerning the composite estimates of abundance and biomass for all and common pool species must be tempered because of the differences in catchability among species (Fraser et al., 2007). However, as was the intention of the analysis design, we feel we can support conclusions related to individual size since the trends in composite estimates are supported among the trends for individual species. The estimates associated with the composite and species trends are for the community of species seen by the survey trawl gear, so there are species and aspects of the food web that are not censused in the analyses. This would include large pelagic species like tunas and billfish that are able to avoid or are not retained by the gear. These taxa are known to use this and other similar ecosystems in the North Atlantic, so the changes in abundance and size of species in the NES will have an impact on the adaptation of large pelagic species in terms of their distribution and productivity (Merino et al., 2019). For

example, declining bluefin tuna condition in the NES has been attributed to reduced size of Atlantic herring, a key prey species (Golet et al., 2015). The same argument can be made for seabirds (Scopel et al., 2019) and a range of marine mammals (Pershing et al., 2021).

Other hypotheses have been made regarding the observed shifts in size of species occupying the northeast continental shelf. Past work using similar data sources theorized that overfishing created a reduction in predator sizes that resulted in reduced predation pressure, combined with increased stratification that enhanced growing conditions for prey fish and led to increased prey biomass from 1970 to 2008 (Shackell et al., 2010). A trophic reshuffling and mild trophic cascade was inferred from the analyses of declines in length and mass across five functional groups and a linear model relating predictors to the aggregate prey biomass (Shackell et al., 2010). Interestingly, while the proposed mechanism for declining prey size and increasing prey biomass was the declining predator size and per capita predation rate, there was no improvement to the models by including lags, and in effect, all the functional groups had observed declines in size and mass over the whole time period (Shackell et al., 2010). These results are similar to those seen here, with systemic declines across species, although the hypothesized mechanisms differ.

Retrospective change in body size, and the possibility of continued change in size in the future, of a broad spectrum of the fish and macroinvertebrates of the NES will change the foraging dynamics of migratory and resident large body predators including large pelagic fish, seabirds, and marine mammals. Smaller prey items present different capture and handling challenges related to their size and motility. While fish swimming speed increases with length, smaller fish accelerate faster and have better turning performance making them more elusive prey items (Domenici, 2001; Domenici and Blake, 1997; Wardle, 1975). The size of the prey also affects the predator's energy expenditure per food item. For example, to reduce energy expenditure during the winter months, Great Cormorants (*Phalacrocorax carbo carbo*) reduced their time spent at sea and selected fewer but larger fish (Johansen et al., 2001). However, when large prey were unavailable to meet their dietary needs, they began fishing earlier and more evenly throughout the day, catching a more variable number of fish with lower mass (Johansen et al., 2001). Many factors control the nutritional quality of prey items, but whether it is viewed from measures of caloric or lipid content, energy density per item must at some level be related to prey item size (Thorvald et al., 2021). Regardless of fish length, our ability to predict the changing dynamics of predator-prey interactions is hampered by the combined impacts of multiple stressors (e.g., increasing temperature, hypoxia, and acidification) on both predator and prey behavior (Domenici, 2001; Domenici et al., 2019).

Fisheries management in the United States is generally based on achieving long-term sustainable yield of total harvested biomass. Changes in body size will have considerable impacts on reference points used in fisheries management, and on any gear-based controls. In a system where much of the catch is unmarketable bycatch (Bell et al., 2017), there is an added burden on harvesters in terms of time and labor associated with operations, and fuel consumption to achieve the same marketable catch (Kleisner et al., 2017). These operators may be faced with a decision of diminishing returns as to when fishing becomes unprofitable. Ecosystem changes such as an overall body size decline also make it more of a challenge to evaluate stock status and for a stock unit to recover from overfishing (Hilborn et al., 2020). Many stocks in the Gulf of Maine and Georges Bank, such as the regionally iconic Atlantic cod, have been resistant to stock rebuilding measures from an overfished status leading to a perception of changed stock productivity. Reasonable application of factors related to biological oceanography and species specific recruitment mechanisms may provide the explanatory reason for rebuilding failure (Pershing et al., 2015). However, we feel the decision-making process may also want to consider species in the context of what tropicalization of the NES may mean for stock productivity (Mendenhall et al., 2020) and the knock-on effects on harvesters

and the overall seafood industry. Continuing with the cod example, we have to include in the set of possible reasons for failed stock recovery the notion that this species, along with others, is now facing increased competition for food and habitat. With growth and reproductive output of individual cod diminished, and the species facing increased competition, stock recovery is less likely. Ecosystem productivity and services are likely to continue changing over time as a more diverse and smaller body size fish and macroinvertebrate community is established. Fisheries management will have to be adapted to meet these challenges, as will the regulatory framework related to bycatch, in order to advance sustainability of catches.

Declaration of competing interest

The authors have declared that no competing interests exist.

Data availability

Data will be made available on request.

Acknowledgements

We thank the many scientists and crewmembers that have helped in collecting high-quality bottom trawl data since its inception.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.166117>.

References

- Arimitsu, M.L., Piatt, J.F., Hatch, S., Suryan, R.M., Batten, S., Bishop, M.A., Campbell, R. W., Coletti, H., Cushing, D., Gorman, K., Hopcroft, R.R., Kuletz, K.J., Marsteller, C., McKinstry, C., McGowan, D., Moran, J., Pegau, S., Schaefer, A., Schoen, S., Straley, J., von Biela, V.R., 2021. Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. *Glob. Chang. Biol.* 27, 1859–1878. <https://doi.org/10.1111/gcb.15556>.
- Audzijonyte, A., Richards, S.A., Stuart-Smith, R.D., Pecl, G., Edgar, G.J., Barrett, N.S., Payne, N., Blanchard, J.L., 2020. Fish body sizes change with temperature but not all species shrink with warming. *Nat. Ecol. Evol.* 4, 809–814. <https://doi.org/10.1038/s41559-020-1171-0>.
- Balch, W.M., Drapeau, D.T., Bowler, B.C., Record, N.R., Bates, N.R., Pinkham, S., Garley, R., Mitchell, C., 2022. Changing hydrographic, biogeochemical, and acidification properties in the Gulf of Maine as measured by the Gulf of Maine North Atlantic time series, GNATS, between 1998 and 2018. *Journal of Geophysical Research: Biogeosciences* 127, e2022JG006790. <https://doi.org/10.1029/2022JG006790>.
- Batt, R.D., Morley, J.W., Selden, R.L., Tingley, M.W., Pinsky, M.L., 2017. Gradual changes in range size accompany long-term trends in species richness. *Ecol. Lett.* 20, 1148–1157. <https://doi.org/10.1111/ele.12812>.
- Baudron, A.R., Needle, C.L., Rijnsdorp, A.D., Tara Marshall, C., 2014. Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Glob. Chang. Biol.* 20, 1023–1031. <https://doi.org/10.1111/gcb.12514>.
- Bell, R.J., Gervelis, B., Chamberlain, G., Hoey, J., 2017. Discard estimates from self-reported catch data: an example from the US northeast shelf. *N Am J Fish Manage* 37, 1130–1144. <https://doi.org/10.1080/02755947.2017.1350219>.
- Boveng, P.L., Ziel, H.L., McClintock, B.T., Cameron, M.F., 2020. Body condition of phocid seals during a period of rapid environmental change in the Bering Sea and Aleutian Islands, Alaska. *Deep Sea Research Part II: Topical Studies in Oceanography*, The lack of Sea-ice Cover and the Northern Bering Sea Marine Ecosystem 181–182, 104904. <https://doi.org/10.1016/j.dsr2.2020.104904>.
- Carozza, D.A., Bianchi, D., Galbraith, E.D., 2019. Metabolic impacts of climate change on marine ecosystems: implications for fish communities and fisheries. *Glob. Ecol. Biogeogr.* 28, 158–169. <https://doi.org/10.1111/gcb.12832>.
- Chassot, E., Bonhommeau, S., Dulvy, N.K., Melin, F., Watson, R., Gascuel, D., Le Pape, O., 2010. Global marine primary production constrains fisheries catches. *Ecol. Lett.* 13, 495–505. <https://doi.org/10.1111/j.1461-0248.2010.01443.x>.
- Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W.Y., Palomares, M. L.D., Watson, R., Pauly, D., 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nat. Clim. Chang.* 3, 254–258. <https://doi.org/10.1038/Nclimate1691>.
- Cheung, W.W.L., Frölicher, T.L., Lam, V.W.Y., Oyinlola, M.A., Reygondeau, G., Sumaila, U.R., Tai, T.C., Teh, L.C.L., Wabnitz, C.C.C., 2021. Marine high temperature extremes amplify the impacts of climate change on fish and fisheries. *Science. Advances* 7, eabh0895. <https://doi.org/10.1126/sciadv.abh0895>.
- Dean, M.J., Hoffman, W.S., Buchan, N.C., Cadrin, S.X., Grabowski, J.H., 2021. Deconstructing size selectivity to evaluate the influence of fishery management. *Fish. Res.* 234, 105782. <https://doi.org/10.1016/j.fishres.2020.105782>.
- Desprespataño, L.I., Azarovitz, T.R., Byrne, C.J., 1988. 25 years of fish surveys in the Northwest Atlantic - the NMFS northeast fisheries centers bottom trawl survey program. *Mar. Fish. Rev.* 50, 69–71.
- Dias, B.S., Frisk, M.G., Jordaan, A., 2019. Opening the tap: increased riverine connectivity strengthens marine food web pathways. *PLoS One* 14, e0217008. <https://doi.org/10.1371/journal.pone.0217008>.
- Domenici, P., 2001. The scaling of locomotor performance in predator–prey encounters: from fish to killer whales. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 131, 169–182. [https://doi.org/10.1016/S1095-6433\(01\)00465-2](https://doi.org/10.1016/S1095-6433(01)00465-2).
- Domenici, P., Blake, R., 1997. The kinematics and performance of fish fast-start swimming. *J. Exp. Biol.* 200, 1165–1178. <https://doi.org/10.1242/jeb.200.8.1165>.
- Domenici, P., Allan, B.J.M., Lefrançois, C., McCormick, M.I., 2019. The effect of climate change on the escape kinematics and performance of fishes: implications for future predator–prey interactions. *Conservation. Physiology* 7, cozo78. <https://doi.org/10.1093/conphys/cozo78>.
- Doney, S.C., Ruckelshaus, M., Emmett Duffy, J., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., Polovina, J., Rabalais, N.N., Sydeman, W.J., Talley, L.D., 2012. Climate change impacts on marine ecosystems. *Annu. Rev. Mar. Sci.* 4, 11–37. <https://doi.org/10.1146/annurev-marine-041911-111611>.
- Eddy, T.D., Bernhardt, J.R., Blanchard, J.L., Cheung, W.W.L., Colléter, M., du Pontavice, H., Fulton, E.A., Gascuel, D., Kearney, K.A., Petrik, C.M., Roy, T., Rykaczewski, R.R., Selden, R., Stock, C.A., Wabnitz, C.C.C., Watson, R.A., 2021. Energy flow through marine ecosystems: confronting transfer efficiency. *Trends Ecol. Evol.* 36, 76–86. <https://doi.org/10.1016/j.tree.2020.09.006>.
- Farr, E.R., Johnson, M.R., Nelson, M.W., Hare, J.A., Morrison, W.E., Lettrich, M.D., Vogt, B., Meaney, C., Howson, U.A., Auster, P.J., Borsuk, F.A., Brady, D.C., Cashman, M.J., Colarusso, P., Grabowski, J.H., Hawkes, J.P., Mercaldo-Allen, R., Packer, D.B., Stevenson, D.K., 2021. An assessment of marine, estuarine, and riverine habitat vulnerability to climate change in the northeast U.S. *PLoS One* 16, e0260654. <https://doi.org/10.1371/journal.pone.0260654>.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49. <https://doi.org/10.1017/S0376892997000088>.
- Fisher, J.A.D., Frank, K.T., Leggett, W.C., 2010. Breaking Bergmann's rule: truncation of Northwest Atlantic marine fish body sizes. *Ecology* 91, 2499–2505. <https://doi.org/10.1890/09-1914.1>.
- Fraser, H.M., Greenstreet, S.P.R., Piet, G.J., 2007. Taking account of catchability in groundfish survey trawls: implications for estimating demersal fish biomass. *ICES J. Mar. Sci.* 64, 1800–1819. <https://doi.org/10.1093/icesjms/fsm145>.
- Friedland, K.D., 2021. A test of the provisioning hypothesis of recruitment control in Georges Bank haddock. *Can. J. Fish. Aquat. Sci.* 78, 655–658. <https://doi.org/10.1139/cjfas-2020-0453>.
- Friedland, K.D., Stock, C., Drinkwater, K.F., Link, J.S., Leaf, R.T., Shank, B.V., Rose, J.M., Pilskaln, C.H., Fogarty, M.J., 2012. Pathways between primary production and fisheries yields of Large marine ecosystems. *PLoS One* 7, 1–11. <https://doi.org/10.1371/journal.pone.0028945>.
- Friedland, K.D., McManus, M.C., Morse, R.E., Link, J.S., 2019. Event scale and persistent drivers of fish and macroinvertebrate distributions on the northeast US shelf. *ICES J. Mar. Sci.* 76, 1316–1334. <https://doi.org/10.1093/icesjms/isy167>.
- Friedland, K.D., Langan, J.A., Large, S.I., Selden, R.L., Link, J.S., Watson, R.A., Collie, J. S., 2020a. Changes in higher trophic level productivity, diversity and niche space in a rapidly warming continental shelf ecosystem. *Sci. Total Environ.* 704, 135270. <https://doi.org/10.1016/j.scitotenv.2019.135270>.
- Friedland, K.D., Morse, R.E., Manning, J.P., Melrose, D.C., Miles, T., Goode, A.G., Brady, D.C., Kohut, J.T., Powell, E.N., 2020b. Trends and change points in surface and bottom thermal environments of the US northeast continental shelf ecosystem. *Fish. Oceanogr.* 29, 396–414. <https://doi.org/10.1111/fog.12485>.
- Friedland, K.D., Morse, R.E., Shackell, N., Tam, J.C., Morano, J.L., Moisan, J.R., Brady, D.C., 2020c. Changing physical conditions and lower and upper trophic level responses on the US northeast shelf. *Front. Mar. Sci.* 7.
- Friedland, K.D., Bachman, M., Davies, A., Frelat, R., McManus, M.C., Morse, R., Pickens, B.A., Smoliński, S., Tanaka, K., 2021a. Machine Learning Highlights the Importance of Primary and Secondary Production in Determining Habitat for Marine Fish and Macroinvertebrates. *Marine and Freshwater Ecosystems n/a, Aquatic Conservation.* <https://doi.org/10.1002/aqc.3527>.
- Friedland, K.D., Methratta, E.T., Gill, A.B., Gaichas, S.K., Curtis, T.H., Adams, E.M., Morano, J.L., Crear, D.P., McManus, M.C., Brady, D.C., 2021b. Resource occurrence and productivity in existing and proposed wind energy lease areas on the Northeast US Shelf. *Frontiers in Marine Science* 8.
- Friedland, K.D., Smoliński, S., Tanaka, K.R., 2021c. Contrasting patterns in the occurrence and biomass centers of gravity among fish and macroinvertebrates in a continental shelf ecosystem. *Ecology and Evolution* 11, 2050–2063. <https://doi.org/10.1002/ece3.7150>.
- Friedland, K.D., Tanaka, K.R., Smoliński, S., Wang, Y., Hodgson, C., Mazur, M., Wiedenmann, J., Goetsch, C., Pendleton, D.E., 2023. Trends in area of occurrence and biomass of fish and macroinvertebrates on the northeast U.S. shelf ecosystem. *Marine and Coastal Fisheries* 15, e10235. <https://doi.org/10.1002/mcf2.10235>.
- Gaines, S.D., Costello, C., Owashii, B., Mangin, T., Bone, J., Molinos, J.G., Burden, M., Dennis, H., Halpern, B.S., Kappel, C.V., Kleisner, K.M., Ovando, D., 2018. Improved fisheries management could offset many negative effects of climate change. *Sci. Adv.* 4. <https://doi.org/10.1126/sciadv.aao1378>.

- Gårdmark, A., Huss, M., 2020. Individual variation and interactions explain food web responses to global warming. *Philosophical Transactions of the Royal Society B: Biological Sciences* 375, 20190449. <https://doi.org/10.1098/rstb.2019.0449>.
- Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L., Heinsohn, R., 2011. Declining body size: a third universal response to warming? *Trends Ecol. Evol.* 26, 285–291. <https://doi.org/10.1016/j.tree.2011.03.005>.
- Golet, W.J., Record, N.R., Lehuta, S., Lutcavage, M., Galuardi, B., Cooper, A.B., Pershing, A.J., 2015. The paradox of the pelagics: why bluefin tuna can go hungry in a sea of plenty. *Mar. Ecol. Prog. Ser.* 527, 181–192. <https://doi.org/10.3354/meps11260>.
- Gonçalves Neto, A., Langan, J.A., Palter, J.B., 2021. Changes in the Gulf stream preceded rapid warming of the Northwest Atlantic shelf. *Communications Earth & Environment* 2, 1–10. <https://doi.org/10.1038/s43247-021-00143-5>.
- Goodman, M.C., Carroll, G., Brodie, S., Grüss, A., Thorson, J.T., Kotwicki, S., Holsman, K., Selden, R.L., Hazen, E.L., De Leo, G.A., 2022. Shifting fish distributions impact predation intensity in a sub-Arctic ecosystem. *Ecography* 2022, e06084. <https://doi.org/10.1111/ecog.06084>.
- Grieve, B.D., Hare, J.A., Saba, V.S., 2017. Projecting the effects of climate change on *Calanus finmarchicus* distribution within the U.S. Northeast Continental Shelf. *Scientific Reports* 7, 6264. <https://doi.org/10.1038/s41598-017-06524-1>.
- Griffiths, D., 2020. Foraging habitat determines predator–prey size relationships in marine fishes. *J. Fish Biol.* 97, 964–973. <https://doi.org/10.1111/jfb.14451>.
- Haedrich, R.L., Barnes, S.M., 1997. Changes over time of the size structure in an exploited shelf fish community. *Fish. Res.* 31, 229–239. [https://doi.org/10.1016/S0165-7836\(97\)00023-4](https://doi.org/10.1016/S0165-7836(97)00023-4).
- Hare, J.A., Morrison, W.E., Nelson, M.W., Stachura, M.M., Teeters, E.J., Griffis, R.B., Alexander, M.A., Scott, J.D., Alade, L., Bell, R.J., Chute, A.S., Curti, K.L., Curtis, T.H., Kircheis, D., Kocik, J.F., Lucey, S.M., McCandless, C.T., Milke, L.M., Richardson, D. E., Robillard, E., Walsh, H.J., McManus, M.C., Marancik, K.E., Griswold, C.A., 2016. A vulnerability assessment of fish and invertebrates to climate change on the northeast US continental shelf. *PLoS One* 11. <https://doi.org/10.1371/journal.pone.0146756>.
- Hastings, R.A., Rutterford, L.A., Freer, J.J., Collins, R.A., Simpson, S.D., Genner, M.J., 2020. Climate change drives poleward increases and equatorward declines in marine species. *Curr. Biol.* 30, 1572–1577.e2. <https://doi.org/10.1016/j.cub.2020.02.043>.
- Hilborn, R., Amoroso, R.O., Anderson, C.M., Baum, J.K., Branch, T.A., Costello, C., de Moor, C.L., Faraj, A., Hively, D., Jensen, O.P., Kurota, H., Little, L.R., Mace, P., McClanahan, T., Melnychuk, M.C., Minto, C., Osio, G.C., Parma, A.M., Pons, M., Segurado, S., Szuwalski, C.S., Wilson, J.R., Ye, Y., 2020. Effective fisheries management instrumental in improving fish stock status. *Proc. Natl. Acad. Sci.* 117, 2218–2224. <https://doi.org/10.1073/pnas.1909726116>.
- Hollowed, A.B., Barange, M., Beamish, R.J., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M.G.G., Hare, J.A., Holt, J., Ito, S., Kim, S., King, J.R., Loeng, H., MacKenzie, B.R., Mueter, F.J., Okey, T.A., Peck, M.A., Radchenko, V.I., Rice, J.C., Schirripa, M.J., Yatsu, A., Yamanaka, Y., 2013. Projected impacts of climate change on marine fish and fisheries. *ICES J. Mar. Sci.* 70, 1023–1037. <https://doi.org/10.1093/icesjms/fst081>.
- Holsman, K.K., Hazen, E.L., Haynie, A., Gourguet, S., Hollowed, A., Bograd, S.J., Samhuri, J.F., Aydin, K., 2019. Towards climate resiliency in fisheries management. *ICES J. Mar. Sci.* 76, 1368–1378. <https://doi.org/10.1093/icesjms/fz031>.
- Huang, B., Thorne, P.W., Banzon, V.F., Boyer, T., Chepurin, G., Lawrimore, J.H., Menne, M.J., Smith, T.M., Vose, R.S., Zhang, H.-M., 2017. Extended Reconstructed Sea surface temperature, version 5 (ERSSTv5): upgrades, validations, and Intercomparisons. *J. Clim.* 30, 8179–8205. <https://doi.org/10.1175/JCLI-D-16-0836.1>.
- Huang, M., Ding, L., Wang, J., Ding, C., Tao, J., 2021. The impacts of climate change on fish growth: a summary of conducted studies and current knowledge. *Ecol. Indic.* 121, 106976. <https://doi.org/10.1016/j.ecolind.2020.106976>.
- Ibarbalz, F.M., Henry, N., Brandão, M.C., Martini, S., Busseni, G., Byrne, H., Coelho, L.P., Endo, H., Gasol, J.M., Gregory, A.C., Mahé, F., Rigonato, J., Royo-Llonch, M., Salazar, G., Sanz-Sáez, I., Scalco, E., Soviadan, D., Zayed, A.A., Zingone, A., Labadie, K., Ferland, J., Marec, C., Kandels, S., Picheral, M., Dimier, C., Poulain, J., Pisarev, S., Carmichael, M., Pesant, S., Acinas, S.G., Babin, M., Bork, P., Boss, E., Bowler, C., Cochrane, G., de Vargas, C., Follows, M., Gorsky, G., Grimsley, N., Guidi, L., Hingamp, P., Iudicone, D., Jaillon, O., Kandels, S., Karp-Boss, L., Karsenti, E., Not, F., Ogata, H., Pesant, S., Poulton, N., Raes, J., Sardet, C., Speich, S., Stemmann, L., Sullivan, M.B., Sunagawa, S., Wincker, P., Babin, M., Boss, E., Iudicone, D., Jaillon, O., Acinas, S.G., Ogata, H., Pelletier, E., Stemmann, L., Sullivan, M.B., Sunagawa, S., Bopp, L., de Vargas, C., Karp-Boss, L., Wincker, P., Lombard, F., Bowler, C., Zinger, L., 2019. Global trends in marine plankton diversity across kingdoms of life. *Cell* 179, 1084–1097.e21. <https://doi.org/10.1016/j.cell.2019.10.008>.
- Ikpewe, I.E., Baudron, A.R., Ponchon, A., Fernandes, P.G., 2021. Bigger juveniles and smaller adults: changes in fish size correlate with warming seas. *J. Appl. Ecol.* 58, 847–856. <https://doi.org/10.1111/1365-2664.13807>.
- Johansen, R., Barrett, R.T., Pedersen, T., 2001. Foraging strategies of great cormorants *Phalacrocorax carbo carbo* wintering north of the Arctic circle. *Bird Study* 48, 59–67. <https://doi.org/10.1080/00063650109461203>.
- Kavanaugh, M.T., Rheuban, J.E., Luis, K.M.A., Doney, S.C., 2017. Thirty-three years of ocean benthic warming along the US northeast continental shelf and slope: patterns, drivers, and ecological consequences. *J. Geophys. Res.-Oceans* 122, 9399–9414. <https://doi.org/10.1002/2017jc012953>.
- Kleinsir, K.M., Fogarty, M.J., McGee, S., Hare, J.A., Moret, S., Perretti, C.T., Saba, V.S., 2017. Marine species distribution shifts on the US northeast continental shelf under continued ocean warming. *Prog. Oceanogr.* 153, 24–36. <https://doi.org/10.1016/j.pcean.2017.04.001>.
- Krebs, Charles J., Krebs, Charles Joseph, Krebs, P. of Z.C.J., Krebs, C.L., 1999. *Ecological Methodology*. Benjamin/Cummings.
- Lavin, C.P., Gordó-Vilaseca, C., Costello, M.J., Shi, Z., Stephenson, F., Grüss, A., 2022a. Warm and cold temperatures limit the maximum body length of teleost fishes across a latitudinal gradient in Norwegian waters. *Environ. Biol. Fish* 105, 1415–1429. <https://doi.org/10.1007/s10641-022-01270-4>.
- Lavin, C.P., Gordó-Vilaseca, C., Stephenson, F., Shi, Z., Costello, M.J., 2022b. Warmer temperature decreases the maximum length of six species of marine fishes, crustacean, and squid in New Zealand. *Environ. Biol. Fish* 105, 1431–1446. <https://doi.org/10.1007/s10641-022-01251-7>.
- Le Bris, A., Pershing, A.J., Gaudette, J., Pugh, T.L., Reardon, K.M., 2017. Multi-scale quantification of the effects of temperature on size at maturity in the American lobster (*Homarus americanus*). *Fish. Res.* 186, 397–406. <https://doi.org/10.1016/j.fishres.2016.09.008>.
- Lindmark, M., Ohlberger, J., Gårdmark, A., 2022. Optimum growth temperature declines with body size within fish species. *Glob. Chang. Biol.* 28, 2259–2271. <https://doi.org/10.1111/gcb.16067>.
- Link, J.S., 2007. Underappreciated species in ecology: “ugly fish” in the Northwest Atlantic Ocean. *Ecol. Appl.* 17, 2037–2060. <https://doi.org/10.1890/06-1154.1>.
- Little, A.G., Loughland, I., Seebacher, F., 2020. What do warming waters mean for fish physiology and fisheries? *J. Fish Biol.* 97, 328–340. <https://doi.org/10.1111/jfb.14402>.
- Lotze, H.K., Milewski, I., 2004. Two centuries of multiple human impacts and successive changes in a North Atlantic food web. *Ecol. Appl.* 14, 1428–1447. <https://doi.org/10.1890/03-5027>.
- Lucey, S.M., Fogarty, M.J., 2013. Operational fisheries in New England: linking current fishing patterns to proposed ecological production units. *Fish. Res.* 141, 3–12. <https://doi.org/10.1016/j.fishres.2012.05.002>.
- Lun, D., Fischer, S., Viglione, A., Blöschl, G., 2022. Significance testing of rank cross-correlations between autocorrelated time series with short-range dependence. *J. Appl. Stat.* 0, 1–17. <https://doi.org/10.1080/02664763.2022.2137115>.
- McLean, M., Mouillot, D., Maureaud, A.A., Hattab, T., MacNeil, M.A., Goberville, E., Lindegren, M., Engelhard, G., Pinsky, M., Auber, A., 2021. Disentangling tropicalization and deborealization in marine ecosystems under climate change. *Curr. Biol.* 31, 4817–4823.e5. <https://doi.org/10.1016/j.cub.2021.08.034>.
- Mendenhall, E., Hendrix, C., Nyman, E., Roberts, P.M., Hoopes, J.R., Watson, J.R., Lam, V.W.Y., Sumaila, U.R., 2020. Climate change increases the risk of fisheries conflict. *Mar. Policy* 117, 103954. <https://doi.org/10.1016/j.marpol.2020.103954>.
- Merino, G., Arrizabalaga, H., Arregui, I., Santiago, J., Murua, H., Urziberea, A., Andonegi, E., De Bruyn, P., Kell, L.T., 2019. Adaptation of North Atlantic albacore fishery to climate change: yet another potential benefit of harvest control rules. *Frontiers in marine Science* 6.
- Miller, T.J., Das, C., Politis, P.J., Miller, A.S., Lucey, S.M., Legault, C.M., Brown, R.W., Rago, P.J., 2010. Estimation of albatross IV to Henry B. Bigelow calibration factors. *NEFSC Ref. Doc.* 10-05, 238.
- Murphy, M.A., Evans, J.S., Storfer, A., 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology* 91, 252–261. <https://doi.org/10.1890/08-0879.1>.
- NEFSC Vessel Calibration Working Group, 2007. Proposed vessel calibration studies for NOAA ship Henry B. Bigelow. Northeast Fisheries Science Center reference document 07-12 (Northeast Fisheries Science Center reference document No. 07–12), Northeast Fisheries Science Center reference document.
- Nillos Kleiven, P.J., Espeland, S.H., Olsen, E.M., Abesamis, R.A., Moland, E., Kleiven, A. R., 2019. Fishing pressure impacts the abundance gradient of European lobsters across the borders of a newly established marine protected area. *Proc. R. Soc. B Biol. Sci.* 286, 20182455. <https://doi.org/10.1098/rspb.2018.2455>.
- Nye, J.A., Link, J.S., Hare, J.A., Overholtz, W.J., 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar. Ecol.-Prog. Ser.* 393, 111–129. <https://doi.org/10.3354/Meps08220>.
- Osland, M.J., Stevens, P.W., Lamont, M.M., Brusca, R.C., Hart, K.M., Waddle, J.H., Langtimm, C.A., Williams, C.M., Keim, B.D., Terando, A.J., Reyier, E.A., Marshall, K. E., Loik, M.E., Boucek, R.E., Lewis, A.B., Seminoff, J.A., 2021. Tropicalization of temperate ecosystems in North America: the northward range expansion of tropical organisms in response to warming winter temperatures. *Glob. Chang. Biol.* 27, 3009–3034. <https://doi.org/10.1111/gcb.15563>.
- Pauly, D., 2021. The gill-oxygen limitation theory (GOLT) and its critics. *Science Advances* 7, eabc6050. <https://doi.org/10.1126/sciadv.abc6050>.
- Pauly, D., Hilborn, R., Branch, T.A., 2013. Fisheries: does catch reflect abundance? *Nature* 494, 303–306. <https://doi.org/10.1038/494303a>.
- Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Le Bris, A., Mills, K.E., Nye, J.A., Record, N.R., Scannell, H.A., Scott, J.D., Sherwood, G.D., Thomass, A.C., 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350, 809–812. <https://doi.org/10.1126/science.aac9819>.
- Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Le Bris, A., Mills, K.E., Nye, J.A., Record, N.R., Scannell, H.A., Scott, J.D., Sherwood, G.D., Thomas, A.C., 2016. Response to Comments on “Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery.” *Science* 352, 423–423. doi:<https://doi.org/10.1126/science.aac0463>.
- Pershing, A.J., Alexander, M.A., Brady, D.C., Brickman, D., Curchitser, E.N., Diamond, A. W., McClenahan, L., Mills, K.E., Nichols, O.C., Pendleton, D.E., Record, N.R., Scott, J.D., Staudinger, M.D., Wang, Y., 2021. Climate impacts on the Gulf of Maine ecosystem: a review of observed and expected changes in 2050 from rising temperatures. *Elementa: Science of the Anthropocene* 9. <https://doi.org/10.1525/elementa.2020.00076>.

- Record, N., Kenney, R., Balch, W., Davies, K., Pershing, A., Johnson, C., Stamieszkin, K., Ji, R., Feng, Z., Kraus, S., Kenney, R., Hudak, C., Mayo, C., Chen, C., Salisbury, J., Thompson, C., 2019. Rapid climate-driven circulation changes threaten conservation of endangered North Atlantic right whales. *Oceanog* 32. <https://doi.org/10.5670/oceanog.2019.201>.
- van Rijn, I., Buba, Y., DeLong, J., Kiflawi, M., Belmaker, J., 2017. Large but uneven reduction in fish size across species in relation to changing sea temperatures. *Glob. Chang. Biol.* 23, 3667–3674. <https://doi.org/10.1111/gcb.13688>.
- Rindorf, A., van Deurs, M., Howell, D., Andonegi, E., Berger, A., Bogstad, B., Cadigan, N., Elvarsson, B.P., Hintzen, N., Savina Roland, M., Taylor, M., Trijoulet, V., van Kooten, T., Zhang, F., Collie, J., 2022. Strength and consistency of density dependence in marine fish productivity. *Fish Fish.* 23, 812–828. <https://doi.org/10.1111/faf.12650>.
- Saba, V.S., Griffies, S.M., Anderson, W.G., Winton, M., Alexander, M.A., Delworth, T.L., Hare, J.A., Harrison, M.J., Rosati, A., Vecchi, G.A., Zhang, R., 2016. Enhanced warming of the Northwest Atlantic Ocean under climate change. *J. Geophys. Res.-Oceans* 121, 118–132. <https://doi.org/10.1002/2015jc011346>.
- Savoca, M.S., Brodie, S., Welch, H., Hoover, A., Benaka, L.R., Bograd, S.J., Hazen, E.L., 2020. Comprehensive bycatch assessment in US fisheries for prioritizing management. *Nat. Sustain.* 3, 472–480. <https://doi.org/10.1038/s41893-020-0506-9>.
- Scheld, A.M., Walden, J., 2018. An analysis of fishing selectivity for northeast US multispecies bottom trawlers. *Mar. Resour. Econ.* 33, 331–350. <https://doi.org/10.1086/699712>.
- Scopel, L., Diamond, A., Kress, S., Shannon, P., 2019. Varied breeding responses of seabirds to a regime shift in prey base in the Gulf of Maine. *Mar. Ecol. Prog. Ser.* 626, 177–196. <https://doi.org/10.3354/meps13048>.
- Shackell, N.L., Frank, K.T., Fisher, J.A.D., Petrie, B., Leggett, W.C., 2010. Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. *Proc. R. Soc. B Biol. Sci.* 277, 1353–1360. <https://doi.org/10.1098/rspb.2009.1020>.
- Shackell, N.L., Ricard, D., Stortini, C., 2014. Thermal habitat index of many Northwest Atlantic temperate species stays neutral under warming projected for 2030 but changes radically by 2060. *PLoS One* 9. <https://doi.org/10.1371/journal.pone.0090662>.
- Sheridan, J.A., Bickford, D., 2011. Shrinking body size as an ecological response to climate change. *Nature Clim Change* 1, 401–406. <https://doi.org/10.1038/nclimate1259>.
- Sherman, K., Duda, A.M., 1999. Large marine ecosystems: an emerging paradigm for fishery sustainability. *Fisheries* 24, 15–26. [https://doi.org/10.1577/1548-8446\(1999\)024<0015:Lme>2.0.Co;2](https://doi.org/10.1577/1548-8446(1999)024<0015:Lme>2.0.Co;2).
- Staudinger, M.D., Mills, K.E., Stamieszkin, K., Record, N.R., Hudak, C.A., Allyn, A., Diamond, A., Friedland, K.D., Golet, W., Henderson, M.E., Hernandez, C.M., Huntington, T.G., Ji, R., Johnson, C.L., Johnson, D.S., Jordaan, A., Kocik, J., Li, Y., Liebman, M., Nichols, O.C., Pendleton, D., Richards, R.A., Robben, T., Thomas, A.C., Walsh, H.J., Yakola, K., 2019. It's about time: a synthesis of changing phenology in the Gulf of Maine ecosystem. *Fish. Oceanogr.* 28, 532–566. <https://doi.org/10.1111/fog.12429>.
- Stock, C.A., John, J.G., Rykaczewski, R.R., Asch, R.G., Cheung, W.W.L., Dunne, J.P., Friedland, K.D., Lam, V.W.Y., Sarmiento, J.L., Watson, R.A., 2017. Reconciling fisheries catch and ocean productivity. *P Natl Acad Sci USA* 114, E1441–E1449. <https://doi.org/10.1073/pnas.1610238114>.
- Swain, D.P., Sinclair, A.F., Mark Hanson, J., 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proc. R. Soc. B Biol. Sci.* 274, 1015–1022. <https://doi.org/10.1098/rspb.2006.0275>.
- Takasuka, A., Yoneda, M., Oozeki, Y., 2019. Density dependence in total egg production per spawner for marine fish. *Fish Fish.* 20, 125–137. <https://doi.org/10.1111/faf.12327>.
- Thomas, A.C., Pershing, A.J., Friedland, K.D., Nye, J.A., Mills, K.E., Alexander, M.A., Record, N.R., Weatherbee, R., Henderson, M.E., 2017. Seasonal trends and phenology shifts in sea surface temperature on the north American northeastern continental shelf. *Elem Sci Anth* 5, 1–17. <https://doi.org/10.1525/elementa.240>.
- Thoral, E., Queiros, Q., Roussel, D., Dutto, G., Gasset, E., McKenzie, D.J., Romestaing, C., Fromentin, J.-M., Sarau, C., Teulier, L., 2021. Changes in foraging mode caused by a decline in prey size have major bioenergetic consequences for a small pelagic fish. *J. Anim. Ecol.* 90, 2289–2301. <https://doi.org/10.1111/1365-2656.13535>.
- Tsikliras, A.C., Polymeros, K., 2014. Fish market prices drive overfishing of the big ones. *PeerJ* 2, e638. <https://doi.org/10.7717/peerj.638>.
- Turner, R.E., 2017. Smaller size-at-age menhaden with coastal warming and fishing intensity. *Geo: Geography and Environment* 4, e00044. <https://doi.org/10.1002/geo2.44>.
- Verberk, W.C.E.P., Atkinson, D., Hoefnagel, K.N., Hirst, A.G., Horne, C.R., Siepel, H., 2021. Shrinking body sizes in response to warming: explanations for the temperature–size rule with special emphasis on the role of oxygen. *Biol. Rev.* 96, 247–268. <https://doi.org/10.1111/brv.12653>.
- Walsh, H.J., Richardson, D.E., Marancik, K.E., Hare, J.A., 2015. Long-term changes in the distributions of larval and adult fish in the northeast US shelf ecosystem. *PLoS One* 10. <https://doi.org/10.1371/journal.pone.0137382>.
- Wang, Y., Gharouni, A., Friedland, K.D., Melrose, D.C., 2021. Effect of environmental factors and density-dependence on somatic growth of eastern Georges Bank haddock (*Melanogrammus aeglefinus*). *Fish. Res.* 240, 105954. <https://doi.org/10.1016/j.fishres.2021.105954>.
- Wardle, C.S., 1975. Limit of fish swimming speed. *Nature* 255, 725–727. <https://doi.org/10.1038/255725a0>.
- Weatherdon, L.V., Magnan, A.K., Rogers, A.D., Sumaila, U.R., Cheung, W.W.L., 2016. Observed and projected impacts of climate change on marine fisheries, aquaculture, coastal tourism, and human health: an update. *Front. Mar. Sci.* 3. <https://doi.org/10.3339/fmars.2016.00048>.
- Weiskopf, S.R., Rubenstein, M.A., Crozier, L.G., Gaichas, S., Griffis, R., Halofsky, J.E., Hyde, K.J.W., Morelli, T.L., Morissette, J.T., Muñoz, R.C., Pershing, A.J., Peterson, D.L., Poudel, R., Staudinger, M.D., Sutton-Grier, A.E., Thompson, L., Vose, J., Weltzin, J.F., Whyte, K.P., 2020. Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. *Sci. Total Environ.* 733, 137782. <https://doi.org/10.1016/j.scitotenv.2020.137782>.
- Woods, P.J., 2022. Aligning integrated ecosystem assessment with adaptation planning in support of ecosystem-based management. *ICES J. Mar. Sci.* 79, 480–494. <https://doi.org/10.1093/icesjms/fsab124>.
- Young, T., Fuller, E.C., Provost, M.M., Coleman, K.E., St. Martin, K., McCay, B.J., Pinsky, M.L., 2019. Adaptation strategies of coastal fishing communities as species shift poleward. *ICES J. Mar. Sci.* 76, 93–103. <https://doi.org/10.1093/icesjms/fsy140>.
- Yue, S., Pilon, P., Phinney, B., Cavadias, G., 2002. The influence of autocorrelation on the ability to detect trend in hydrological series. *Hydrol. Process.* 16, 1807–1829. <https://doi.org/10.1002/hyp.1095>.
- Zeller, D., Palomares, M.L.D., Tavakolie, A., Ang, M., Belhabib, D., Cheung, W.W.L., Lam, V.W.Y., Sy, E., Tsui, G., Zyllich, K., Pauly, D., 2016. Still catching attention: sea around us reconstructed global catch data, their spatial expression and public accessibility. *Mar. Policy* 70, 145–152. <https://doi.org/10.1016/j.marpol.2016.04.046>.