

# Diverging phenology of American lobster (*Homarus americanus*) larvae and their zooplankton prey in a warming ocean

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## Abstract

We build on previous research describing correlative links between changes in the abundance of the copepod *Calanus finmarchicus*, a foundational zooplankton species of the pelagic food web, and diminishing recruitment of young-of-year American lobster (*Homarus americanus*) to benthic nurseries in the Gulf of Maine. Using parallel 31-year time series of lobster larvae and zooplankton collected on the New Hampshire coast between 1988 and 2018, we investigated how changes in phenology of stage I larval lobster and their putative copepod prey, *C. finmarchicus*, affect their temporal overlap and potential to interact during the larval season. We found that over the time series both the lobster egg hatch and first appearance of larvae began earlier in the season, a trend significantly correlated with ocean warming. The last appearance of larvae in late summer has been delayed, however, thereby extending the larval season. Even with the longer larval lobster season, the *C. finmarchicus* season has increasingly been ending before the peak abundance of stage I lobster larvae. The net effect is a widening mismatch in phenology of the two species, an outcome consistent with the hypothesis that changes in abundance and phenology of *C. finmarchicus* have contributed to recent declines in lobster recruitment.

**Keywords:** American lobster; phenology; match-mismatch; trophic interactions; predator-prey; zooplankton; neuston net; *Calanus finmarchicus*; larvae; postlarvae

## Introduction

Effects of climate change, including warming, coastal and ocean acidification, and hypoxia, are causing profound alterations to marine ecosystems (Doney et al. 2012, Poloczanska et al. 2016, Pershing et al. 2018) and the productivity and sustainability of important marine resources (Free et al. 2019). In marine invertebrates and fish with planktonic larvae, a warming climate alters the seasonal phenology of reproduction and growth that may have consequences for trophic interactions between the larval stage and critical planktonic food sources, which also change seasonally. Cushing (1969, 1990) invoked the match–mismatch hypothesis (MMH) that suggested that year-class success of planktotrophic species depends on sufficient overlap between a larval cohort and critical planktonic foods. Subsequently, numerous studies have evaluated variation in the seasonal overlap of predator and prey, and attempted to evaluate the link to recruitment success (Mertz and Myers 1994, Durant et al. 2005, 2007, Perretti et al. 2017). Here, we examine the phenology of the American lobster (*Homarus americanus*, hereafter lobster) and the copepod *Calanus finmarchicus* (hereafter *C. finmarchicus* or *Calanus*) and hypothesize that recent dramatic declines in lobster larval survival may be linked not only to declines in the abundance of a critical copepod prey (Carloni et al. 2018) but also to an increasing mismatch in their phenology.

Climate change has altered several coastal fisheries of the Northwest Atlantic and the Gulf of Maine (GoM) (Oviatt 2004, Brander 2010, Cheung et al. 2013, Pinsky and Mantua 2014, Richards and Hunter 2021). Lobster, however, has been thriving in this region, particularly over the past decade, where population levels have increased by 50%, and spawning stock biomass is currently at historic highs (ASMFC 2020). Despite expectations of high larval production from the record levels of egg production over the past decade, young-of-year (YOY) recruitment to coastal nursery grounds has been at record lows in recent years, magnifying the need to better understand the factors that affect survival from egg hatch to settlement, a process that takes roughly 26 days at temperatures of 18°C–21°C, with approximate developmental times for stages I, II, III, and IV of 3, 3, 4, and 16 days, respectively, in lab-reared larvae (MacKenzie 1988, Katz et al. 1994), although there is evidence that developmental rates may be significantly shorter in the wild (Annis et al. 2007).

In our original study, we found that high spawner abundance translated to high early-stage larval production. However, the abundance of pelagic postlarvae and benthic YOY recruits surprisingly showed no correlation with early-stage larval abundance, or with abiotic factors (i.e. temperature, wind advection, and the North Atlantic Oscillation index), but rather was significantly coupled to time trends in the copepod, *C. finmarchicus*, a foundational species of the GoM's

pelagic ecosystem (Carloni et al. 2018). Copepods and other zooplankton have been reported in the diets of wild-caught lobster larvae (Herrick 1895, Juinio and Cobb 1992), and recent DNA sequencing and microscopy by Ascher (2023) and feeding behavior studies by Layland (2023) add to this long-standing relationship, and dispel any doubt that all three lobster larval stages and the postlarval stage readily consume and in some contexts selectively feed on *C. finmarchicus*. This evidence suggests that *Calanus* may be an integral food source for early-stage larvae to complete metamorphosis to the postlarval stage, a biological transformation that requires high-quality nutrition (Eagles et al. 1986, Ascher 2023). Here, we examined the phenology of the putative predator and prey to evaluate whether a widening temporal mismatch together with the documented decline in abundance of *C. finmarchicus* would reinforce the food limitation hypothesis proposed by Carloni et al. (2018).

The GoM is among the fastest-warming bodies of water on the planet (Nye 2010, Mills et al. 2013, Pershing et al. 2015), and phenological shifts have been reported for several species in recent years (Richards 2012, Staudinger et al. 2019). Northern shrimp (*Pandalus borealis*) is at the southern end of its range in the GoM and has become a *de facto* indicator species for the region as the population in the GoM has declined precipitously in the face of a rapidly changing environment (Richards and Hunter 2021). Although the drivers are numerous and their interaction complex, changes in the predator field and shifts in egg hatch phenology have been identified as an important component of the precipitous decline in its population (Richards 2012, Richards and Hunter 2021).

American lobster abundance is currently near historic high levels, though there have been recent notable changes that have coincided with warming waters of the Gulf: (i) population increase and expansion to historically cooler locations in the northeastern GoM and farther offshore (Goode et al. 2019, ASMFC 2020); (ii) declines in the size at maturity (Waller et al. 2019, 2021); and (iii) egg hatch occurring earlier in the spring (Haarr et al. 2018, ASMFC 2020, Goode 2021). Unclear, however, is how changes in the timing of egg hatch affect the temporal overlap with planktonic food sources.

*C. finmarchicus* is a large-bodied copepod (adults: ~2.5–3.0 mm) that widely dominates the zooplankton biomass of the Arctic and boreal North Atlantic (Conover 1988, Williams 1988, Melle et al. 2014, Pepin and Head 2009). The combination of size, abundance, and the high lipid content in the eggs, prefeeding naupliar, and late copepodite stages (Jonasdottir 1999, Lee et al. 2006) makes this species a critically important source of energy for higher trophic levels, including larval fish (Planque and Batten 2000, Beaugrand et al. 2003), crustaceans (Harvey and Morrier 2003), and baleen whales, including the endangered North Atlantic right whale, *Eubalaena glacialis* (Kann and Wishner 1995, Woodley and Gaskin 1996, Baumgartner and Mate 2003, Meyer-Gutbrod et al. 2021).

In the GoM, *C. finmarchicus* has pronounced seasonal and yearly variation in the timing of the hatch and overall abundance (Bigelow 1926, Meise and O'Reilly 1996). The year-to-year variability is driven largely by changes in the local vital rates of the reproducing population rather than through the advection of individuals into or out of the GoM (Mullin 1963, Ji et al. 2022). As a result, changes in environmental conditions (e.g. temperature and food availability) can have direct consequences on the timing and magnitude of the

peak biomass of *C. finmarchicus* each year. In the past two decades, the GoM has been warming at a faster rate than most other coastal regions due to a combination of global temperature rise (Pershing et al. 2015) and changing circulation patterns, including a weakening influence of the cold, nutrient-rich Labrador Current from the north, and a strengthening influence of the warm, salty, and nutrient-poor Gulf Stream (Record et al. 2019, Friedland et al. 2020, Gancalvez-Neto et al. 2021, Townsend et al. 2023). These environmental changes are influencing the phenology of *C. finmarchicus* throughout the GoM, which has increased production in the spring, but decreased production during the summer in recent years (Record et al. 2019). This summer period is a critical time for lobster as females are hatching eggs, and larval survival to the postlarval stage has been strongly linked to food quality and quantity (Eagles et al. 1986). Changing phenology of predator and prey species can lead to a mismatch in their temporal overlap, and thus affect larval condition and survival (Cushing 1990).

As climate change continues to have far-reaching effects on coastal ecosystems, it is paramount to gain a comprehensive understanding of the processes that affect recruitment and the sustainability of North America's most valuable single-species commercial fishery. This research builds on our previous studies describing the correlative links between changes in the abundance of *C. finmarchicus* and recruitment of YOY lobster to benthic nurseries in the GoM (Carloni et al. 2018, ASMFC 2020, Wahle et al. 2021). Here, we assess how changes in phenology over a three-decade time series have altered the temporal overlap of adult *C. finmarchicus* and larval lobsters during the spring and summer and speculate on the implications of this widening mismatch for lobster recruitment.

## Methods

### Study area and data sources

We evaluated phenology shifts of lobster egg hatch, larvae, and zooplankton from the following concurrent monitoring programs conducted off the New Hampshire coast, USA (Supplemental Fig. 1).

### Commercial sea sampling

New Hampshire Fish and Game Department conducted monthly sampling of the commercial lobster catch from NOAA Statistical Area (SA) 513 from May to November at three areas along the New Hampshire coastline from 2002 to 2017 (Supplemental Fig. 1). Sampling was conducted during day trips on commercial lobster boats fishing in New Hampshire waters, where a variety of biological data were collected, including developmental stage of eggs. Egg-bearing lobsters with visible signs of empty egg casings, visible mossy-appearing cementum, and/or visible prezoaeae were classified as hatching (Haarr et al. 2023). A full description of the egg-staging technique used in this study can be found online (<https://www.youtube.com/watch?v=cJogiaAofCg>).

### Zooplankton and larval lobster sampling

Normandeau Associates, Inc. has conducted zooplankton and larval lobster monitoring off the New Hampshire coast since 1978 as part of ongoing environmental impact studies. Zooplankton were sampled at three stations using oblique tows with a pair of 1-m-diameter plankton hoop nets (505  $\mu$ m

mesh) (Supplemental Fig. 1). Nets were fitted with depressors to keep the nets horizontal and flow meters and towed for 10 min under variable speeds to allow nets to sample the majority of the water column with each tow sampling a volume of  $\sim 500 \text{ m}^3$ . Samples were collected monthly from 1988 to 2018 and fixed in buffered formalin before enumeration. To sample lobster larvae, a neuston net (1000  $\mu\text{m}$ ) was deployed with depressors to keep the net horizontal while sampling the top 0.5 m of the water column. Thirty-minute tows were made during the day, sampling an average area of  $\sim 3730 \text{ m}^2$  (a volume of  $1865 \text{ m}^3$ ). Tows were conducted weekly from May to October. In our analysis, we used weekly mean values for stage I and postlarval (stage IV) abundance from 1988 to 2018 due to consistency in sampling during that time period. We did not analyze trends in stage II and stage III larvae as these stages are rarely caught in this survey likely because they are primarily found at greater depths than are sampled by a neuston net (Harding et al. 1987). Additionally, bottom water temperatures were used from two sources: (i) Normandeau from 1988 to 2018 at two stations collected four times per month to assess correlative relationships with first appearance of stage I and (ii) NERACOOS Western Maine Shelf Buoy B (20 m) to assess relationships with egg hatch. For these analyses, we used the mean temperatures from April to June as spring warming has been shown to influence the timing of egg hatch (Goldstein and Watson 2015).

### Statistical analysis

Proportion of eggs hatching was calculated by dividing the number of egg-bearing lobster in the process of hatching by the total number of egg-bearing lobsters within the same year class (i.e. predicted to hatch within the same year). We used Pearson's correlation coefficient ( $r$ ) to assess linear relationships between variables. In cases where variables violated the normality assumption (as assessed via a Shapiro–Wilk test), Spearman's rank test was used. Time-series trends were assessed using Mann–Kendall, and deemed significant at the  $P < 0.05$  level; additionally, autocorrelation was tested using a Durbin–Watson test. Due to differences in sampling frequency, changes in phenology of lobster larvae were assessed on a weekly basis, whereas trends in *C. finmarchicus* were assessed by 2-week blocks, which were expressed as time periods (e.g. time period 1 = first two weeks of January). For lobster larvae, we defined first and last appearances as first and last catch of each season and duration as time between first and last catch. We defined the start of *C. finmarchicus* season as the time period where the 25th percentile of the cumulative annual index was reached, the end of the season as the 75th percentile, and the duration as the 25th–75th percentile.

We also evaluated the degree of overlap between the larval lobster and *C. finmarchicus* season using a mismatch index modeled after Burthe et al. (2012), assessing the difference in time between peak stage I lobster larval abundance and the end of the *C. finmarchicus* season as follows:

Week of year *C. finmarchicus* reached 75th percentile – week of year of peak abundance of stage I = # of weeks of match or mismatch.

Negative values represent a potential mismatch, while positive values suggest a higher level of temporal overlap. Stage I larvae were chosen for this analysis as food quality and quantity have been shown to influence survival rates of early-

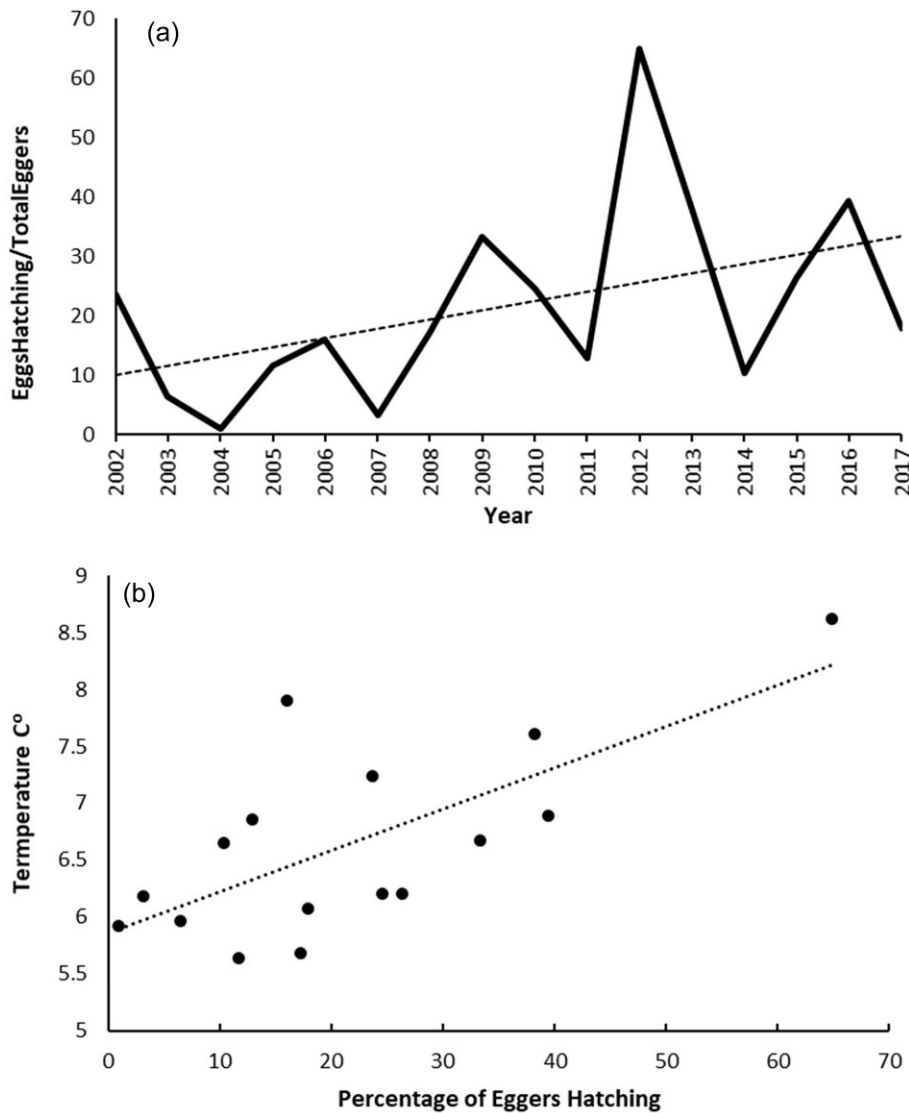
stage larvae (Anger et al. 1985, Eagles et al. 1986), whereas postlarval lobsters are more resistant to starvation due to energy reserves (Juinio and Cobb 1992, Ascher 2023). Foundational time series (1988–2018) for stage I and postlarval lobster larvae, as well as *C. finmarchicus*, can be found in Supplemental Fig. 2. All data were analyzed using the statistical software package JMP Pro 16.1.0.

### Results

Between 2002 and 2017, egg hatch peaked in July a majority of time (69%), followed by June (31%). June also represents the predominant month eggs begin to hatch, which has trended significantly upward with a 3-fold increase over time (Fig. 1a, Mann–Kendall:  $P < 0.05$ ). The earlier onset of hatching correlates significantly with warming mean spring bottom temperatures (April–June) over the period (Fig. 1b, Pearson's:  $r = 0.7013$ ,  $P = 0.0025$ ). Accordingly, the first appearance of stage I larvae (Fig. 2a) has occurred significantly earlier in the season (Mann–Kendall  $P = 0.007$ ), which also correlates with spring temperature (Spearman's  $-0.4344$ ,  $P = 0.0011$ ). Interestingly, in recent years, stage I larvae have not only appeared earlier but also been present later (Fig. 2b), resulting in a longer season duration (Fig. 2c, Mann–Kendall:  $P = 0.001$ ). In contrast to the stage I larvae, the first appearance, last appearance, and season duration of postlarvae have varied without trend over the time series (Mann–Kendall  $\geq 0.0$ ); however, because stage I larvae have been appearing earlier in the season, the total larval season duration (first appearance of stage I to last appearance of postlarvae) has significantly increased (Fig. 2d, Mann–Kendall:  $P = 0.009$ ), resulting in an inverse correlation between the date of first appearance of stage I and total larval season duration (Pearson's  $r = -0.5004$ ,  $P = 0.0067$ ).

The onset of the *C. finmarchicus* season has varied without trend over the 31-year time series (Mann–Kendall:  $P \geq 0.05$ ); however, the end of season has tended to come earlier in recent years, resulting in significantly shorter seasons (Figs 3a and b; Mann–Kendall:  $P = 0.02$ ). As previously stated, in most years lobster eggs hatch in July. We also found the strongest correlation between monthly abundance of *C. finmarchicus* and postlarval lobsters to occur in July and August (Table 1), suggesting that these summer months may be a critical period for earlier stage larvae to access high-quality food that is necessary for reaching the postlarval stage. Not only the *C. finmarchicus* season duration has become shorter but since 2012 it has also ended (reached 75th percentile) before this critical period begins (1 July) in six of the seven years, coupled with sustained low levels of abundance after 1 July (Fig. 3a and c). In short, the earlier end to the *C. finmarchicus* season has been outpacing the earlier start to the lobster larval season.

Seasonal peaks in abundance for both stage I and postlarvae remained stable throughout the time series (Mann–Kendall:  $P \Rightarrow 0.05$ ), whereas *C. finmarchicus* showed a significant trend toward peaking earlier in the season (Mann–Kendall:  $P < 0.022$ ; Supplemental Fig. 3). Differences in the timing of the peak in stage I lobster larval abundance and the *C. finmarchicus* season were integrated into a mismatch index (Fig. 4a), which trended downward (i.e. reduced temporal overlap) over the time series (Mann–Kendall:  $P = 0.039$ ). Between 1999 and 2008, stage I larvae tended to peak well within the *C. finmarchicus* season (mismatch index average = +3.4 weeks) coinciding with a period of high postlarval



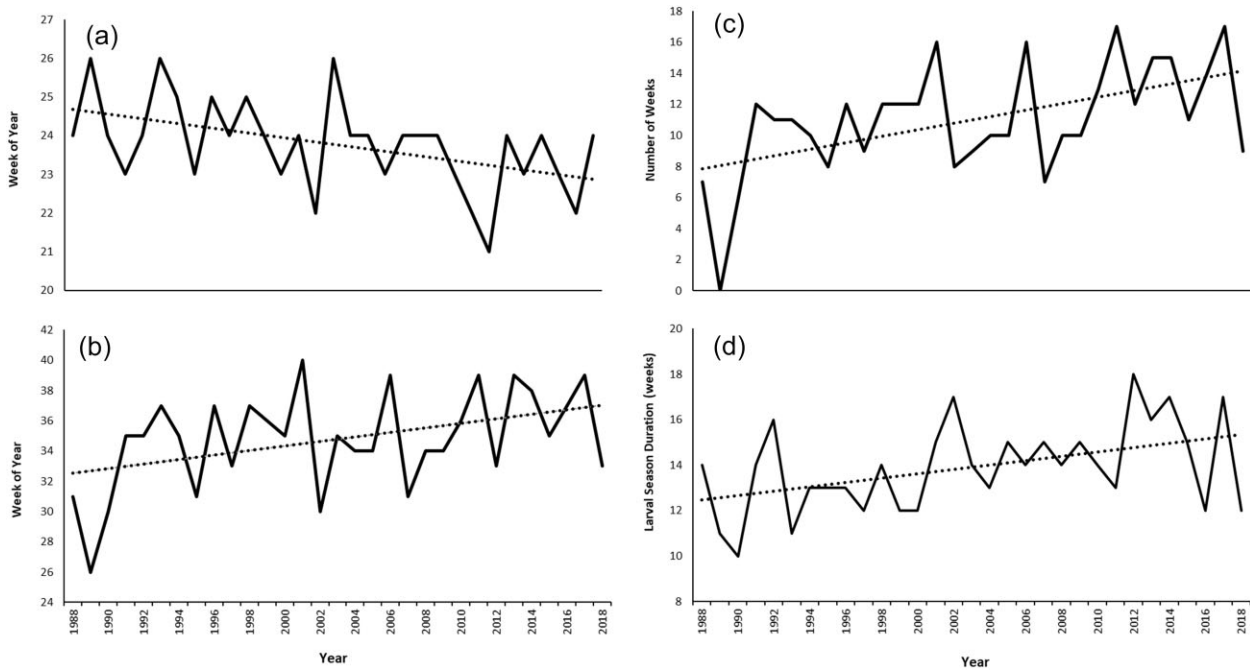
**Figure 1.** (a) Percentage of egg-bearing lobsters with eggs in the process of hatching in the month of June, from commercial lobster sea sampling in New Hampshire coastal waters from 2002 to 2017. (b) Relationship between percentage of egg-bearing lobsters hatching in June and mean bottom water temperature (20 m) from April to June (2002–2017).

abundance. In contrast, from 2009 to 2018, stage I larvae peaked well after the *C. finmarchicus* season ended (mismatch index average =  $-2.6$  weeks), which coincides with a period of low postlarval abundance (Fig. 4b). Changes in temporal overlap grouped by decade are also evident in the proportion of catch by time period. During the first two decades, 1989–1998 and 1999–2008, there was strong temporal overlap denoted by positive values of the index, but in the last time segment, 2009–2018, the *C. finmarchicus* season ended earlier, causing a widening mismatch compared to the previous two decades (Figs 4b and 5). In addition to this apparent divergence in overlap, there has been a 70% decline in the abundance of *Calanus* during the larval season in the most recent decade.

## Discussion

It has long been known that lobster larvae feed on copepods (Herrick 1911, Harding et al. 1983), and our observations, as well as recent molecular and behavioral research,

confirm that all four planktonic stages can capture and ingest adult *C. finmarchicus* (Ascher 2023, Layland 2023), a species that has significantly more lipid reserves compared to some other common copepods in the region (DeLorenzo Costa et al. 2006, Ascher 2023). In fact, there is evidence that *C. finmarchicus* may be a preferred prey item (Layland 2023) in certain contexts. Thus, changes in the abundance and relative timing between peak larval abundance and this energy-rich copepod may have a profound impact on larval survival, resulting in recruitment success of lobster. Using a 31-year time series collected on the New Hampshire coast, we found links between ocean warming, the timing of lobster egg hatch, and the first appearance of stage I larvae that indicate an earlier onset and lengthening of the larval season. Through the parallel zooplankton time series, we were also able to quantify the phenological shift in *C. finmarchicus* to reveal an increasing mismatch (Cushing 1990, Burthe et al. 2012) between the two species, especially over the past decade (2009–2018). Our data show an increasing gap of time between the end of the *C. finmarchicus* season and the time of peak of stage I



**Figure 2.** Shifts in larval lobster phenology. (a) Larval stage I first appearance, (b) last appearance, (c) stage I season duration, and (d) total larval season duration through the postlarval stage, from neuston net sampling along the New Hampshire coast, 1988–2018. Dotted lines are fitted trend lines.

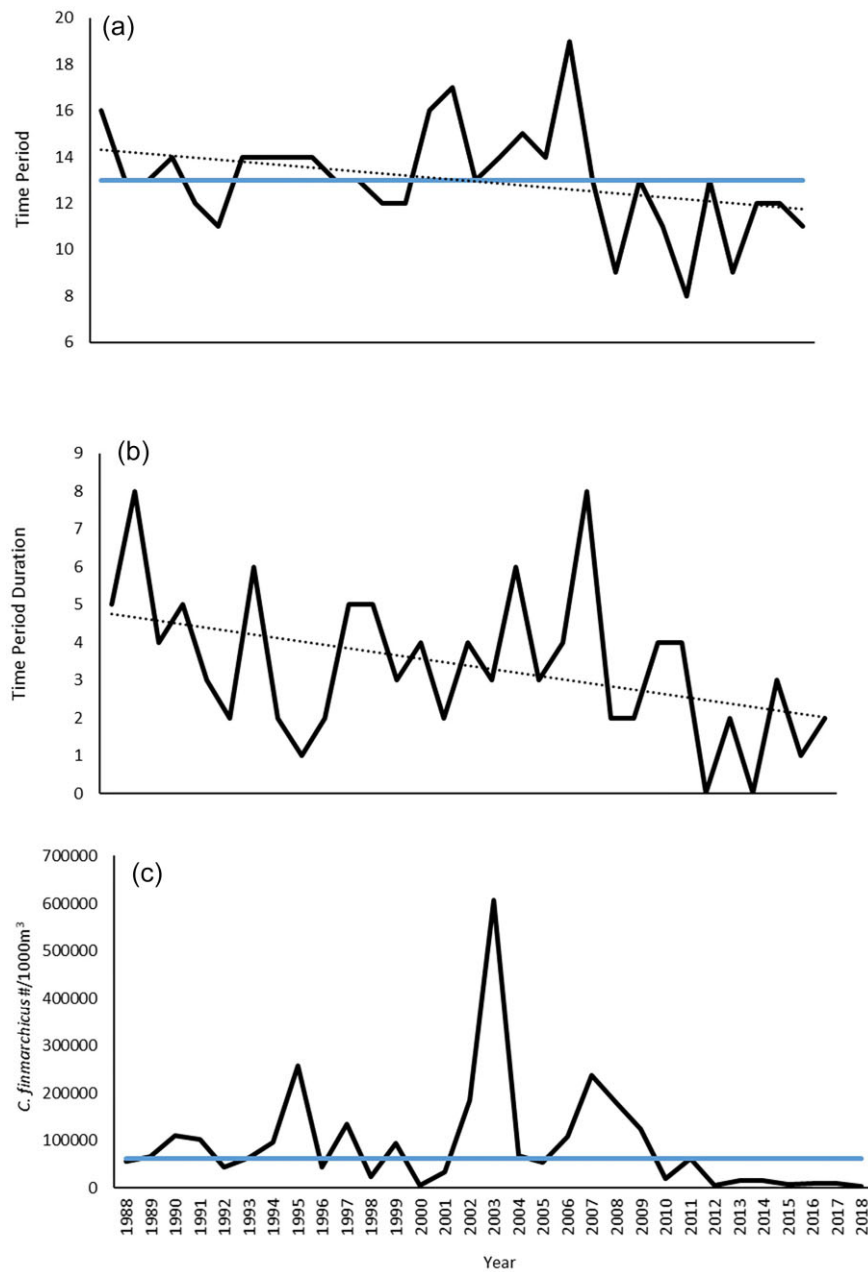
lobster larval abundance. We speculate that the reduced temporal overlap between planktonic larval lobsters and *C. finmarchicus* could exacerbate the impact of already declining abundance of *C. finmarchicus* on lobster larval survival and YOY recruitment in the GoM as suggested by the correlations in Carloni et al. (2018) and Wahle et al. (2021).

The significant increase in spring temperatures correlates well with timing of egg hatch and supports the hypothesis that recent warming is an important factor influencing rapid changes in the timing of this critical biological event. Accordingly, stage I larvae have been appearing earlier in the season, but counter to expectations, the last appearance of this stage has occurred later in the season, resulting in a longer season duration. Similarly, in response to warming waters at the southern extreme of its range in the GoM, the northern shrimp has been hatching earlier and exhibiting an extended larval season, which could be beneficial by increasing the window of opportunity for larvae to encounter favorable conditions (Richards 2012). If indeed *Calanus* is an important food source for early-stage larvae, the longer larval season reported in our study does not appear to be advantageous for increased larval survival, as not only is the *Calanus* season ending earlier, particularly during these years of extended larval season duration, but the abundance of this food source remains low throughout the larval season.

We offer two hypotheses that may be playing a role in longer larval season duration. First, lobsters are known to take offshore to inshore seasonal migrations, likely to take advantage of the warmer shallow waters to speed up egg development and thus hatch (Cooper and Uzman 1971, Krouse 1973, Campbell and Stasko 1986, Campbell 1986, Jury et al. 2019), whereby larger females undergo longer migrations and experience different temperatures from smaller ovigerous lobsters (Cowan et al. 2007). There is also evidence that they will move back toward deeper and cooler water once their eggs are ready to hatch (Carloni and Watson 2018, Carloni et al.

2021). These complex reproductive movements, in combination with a rapidly changing environment involving unprecedented spring warming, could result in lobsters of different sizes at varying depths experiencing vastly different temperatures, and thus hatching at more disparate times than in the past. Alternatively, the extended larval season may be an artifact of slower larval developmental times, possibly linked to lower food quality or quantity (Eagles et al. 1986, Ascher 2023). Although larvae can molt to postlarval stage with lower quality food, stage duration is shorter and survival rate increases with higher quality foods.

Lobster larval development and survival has been strongly linked to food quality and quantity in the laboratory (Templeman 1936, Eagles et al. 1986, Ascher 2023). To date, there are only a few published studies of larval diets from field collections (Herrick 1911, Harding et al. 1983, Juinio and Cobb 1992), and there is only one for larvae from the GoM (Ascher 2023). It is difficult to say whether *C. finmarchicus* is a sufficiently important component of the diet of larval lobster to limit survival; however, this copepod has a significantly higher caloric and lipid content than other common copepods in the region (DeLorenzo Costa et al. 2006) and constitutes the primary food for many fish and marine mammals (Kane 1984, Woodley and Gaskin 1996). In addition, laboratory observations indicate that all stages of lobster larvae readily consume *C. finmarchicus* with evidence suggesting a preference for *C. finmarchicus* when given a choice among several copepod species (Layland 2023). Both microscopy and molecular analysis have revealed *C. finmarchicus* in the natural diet (Junio and Cobb 1992, Ascher 2023). General experiments quantifying the feeding rates of lobster larvae on natural diets and focused experiments measuring the feeding rates on different *Calanus* life stages would help fill a clear knowledge gap. Further research is needed to better understand the dynamic driving relationship between trophic interactions and larval development time.

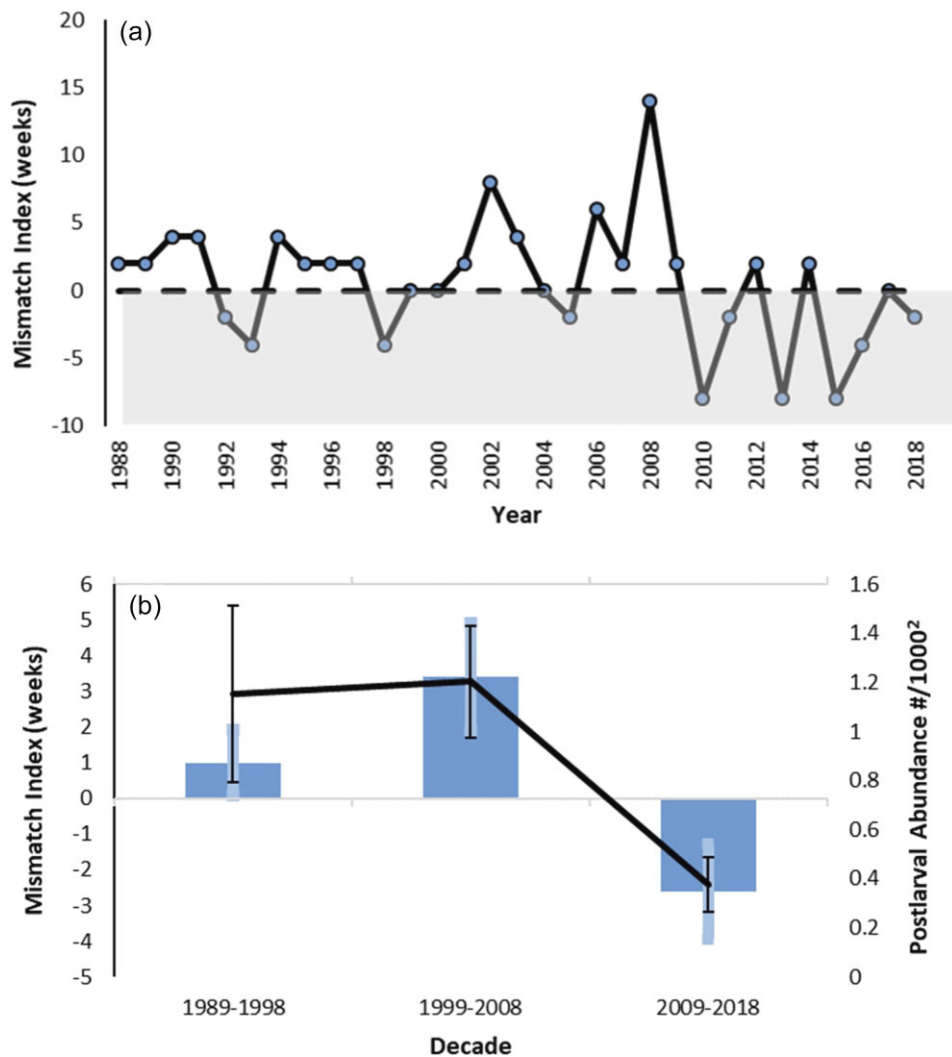


**Figure 3.** Shifts in *C. finmarchicus* phenology. (a) End of season and (b) season duration (2 week blocks) by year from 1988 to 2018. “Time periods” correspond to 2-week blocks. Dotted line is the fitted trendline. Blue horizontal line in A denotes 1 July (time period 13); since 2009, the season has ended on or before that date. (c) *C. finmarchicus* abundance from July to October, demonstrating in concert with (a) that not only has the end of season (75th percentile) been occurring earlier in most recent decade, but abundance has been well below median values (horizontal line) after the critical larval period begins (1 July).

**Table 1.** Correlation statistics by month between *C. finmarchicus* and post-larval lobster abundance in New Hampshire waters, 1988–2018. Note, bold text denotes significant correlations ( $P < 0.05$ ).

Month	Spearman's $r$	$P$
May	0.25	0.1887
June	-0.15	0.4311
<b>July</b>	<b>0.64</b>	<b>0.0002</b>
<b>August</b>	<b>0.58</b>	<b>0.0007</b>
September	0.25	0.1751
October	0.25	0.1806

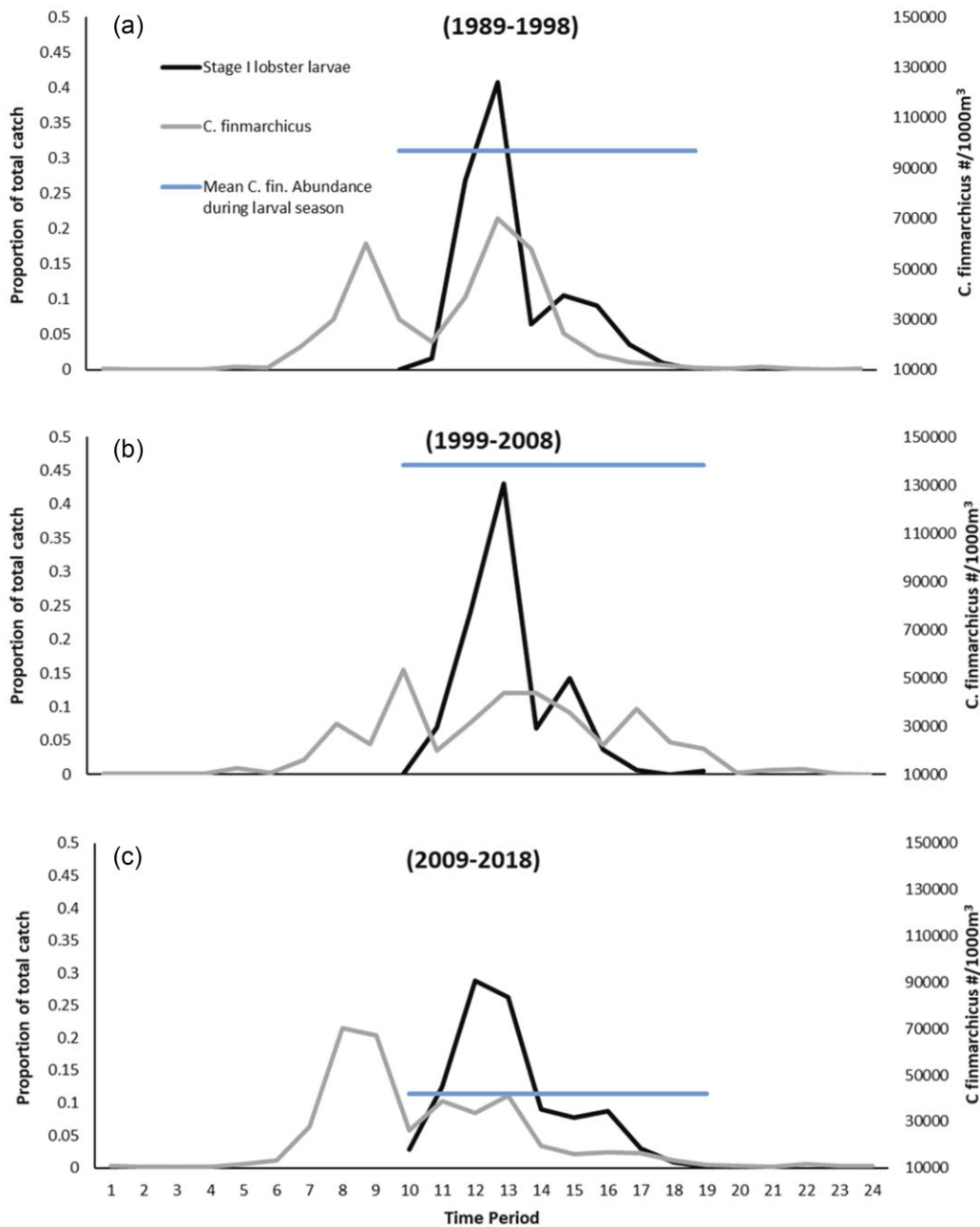
We found several noteworthy relationships between *C. finmarchicus* and early-stage larvae, which give us a better understanding of how the abundance and availability of this food source have changed over time. Over the 31-year time series, we found a significant decline in the temporal overlap of these two species, a mismatch that can more closely be tracked to the most recent decade (2009–2018) of our study. For 2009–2018, the *Calanus* season ended nearly 3 weeks before the peak abundance of lobster stage I larvae in the water column. There has been a 6-week shift in the end of the *Calanus* season from the first to the last decade of our three-decade time series, which means that the *Calanus* season in



**Figure 4.** Mismatch index between larval lobster and *C. finmarchicus* phenology. (a) The decreasing overlap between peak abundance of stage I lobster larvae and the end of the *C. finmarchicus* season. A negative index indicates that peak stage I occurred after the end of *C. finmarchicus* season. The downward trend is statistically significant (Mann-Kendal:  $P = 0.039$ ). (b) Mean mismatch index values by decade over the 30-year time series (bars) and postlarval abundance by decade (black line). Note that postlarval abundance is relatively high in years of greater overlap between peak stage I and *C. finmarchicus*.

recent years has ended well before stage I lobster larvae peak. This widening mismatch in temporal overlap in the most recent decade was also accompanied by a 70% decrease in the abundance of *Calanus* available during the larval season. The compounding effects of changing phenology and declining abundance of this lipid-rich food source could have wide-ranging implications for animals that rely on their energy content for growth and survival (e.g. Conover 1988, Lee et al. 2006, Pepin and Head 2009, Melle et al. 2014). We acknowledge the potential limitations of the small spatial scale of our study in drawing conclusions for the broader GoM ecosystem; however, trends in *Calanus* and their links to lobster recruitment in the western GoM reported in our principal study (Carloni et al. 2018) have since been corroborated by a broad-scale analysis throughout the GoM, including the Bay of Fundy (ASMFC 2020, Wahle et al. 2021). Moreover, phenological shifts and declining summer production of *Calanus* reported here agree with larger basin-scale analyses (Record et al. 2019).

The drivers of *C. finmarchicus* phenology have not been fully resolved. The species has a complex life cycle that includes a dormant (diapause) period where pre-adults accumulate lipids during the summer when food supply and environmental conditions are favorable, and enter diapause in deep water during the fall and early winter when food and environmental conditions are poor, a possible bet-hedging adaptation to survive these conditions until the next spring phytoplankton bloom when they mature to adulthood, mate, and release their eggs (Kaartvedt 2000, Varpe and Fiksen 2010). The proximate cues controlling when *C. finmarchicus* enter diapause are enigmatic. Given the great depth at which diapause occurs (500+ m; Hirche 1996, Heath et al. 2004), it is unlikely that changing light levels are sufficient to initiate the molt to adulthood. This has led some to consider depletion of energy reserves as the trigger for maturation (Häfker et al. 2018, Skottene et al. 2019, Bandara et al. 2021). Because temperature at diapause depth varies little, the onset of the *C. finmarchicus* season has varied without trend over the



**Figure 5.** Decadal differences in the phenology of stage I lobster larvae and *C. finmarchicus* at the coastal New Hampshire sampling sites expressed as proportion present over time. Mean abundance of *C. finmarchicus*/1000 m<sup>3</sup> during the larval season denoted by a horizontal line. Note that the abundance in most recent decade (2009–2018) is 70% lower than that of the previous decade (1999–2008).

31-year time series. Therefore, changes in *C. finmarchicus* phenology are more likely to arise from changes in the developmental rates of the newly hatched *C. finmarchicus*. When the eggs hatch, they ascend the water column and the naupliar larval stages eventually begin to feed, develop, and accumulate fats. Warmer surface temperatures accelerate development of the copepod and result in smaller (Runge et al. 2015, Fields et al. 2022), less fecund, adults (Carlotti and Hirche 1997). As temperatures in the GoM continue to increase (Pershing et al. 2015), and nutrient supplies and phytoplankton decline, *C. finmarchicus* abundance may continue to decline and their phenology may continue to contract.

Although we are beginning to understand the effects of climate change on the oceanography, ecosystem dynamics, and

fisheries of the GoM (Pershing et al. 2015, 2021, Richards et al. 2016, González-Neto et al. 2021), our understanding of the mechanisms at work behind these changes remains largely correlative. In the case of the American lobster, the decoupling of the spawner–postlarval relationship occurs during the early larval stages. We hypothesize that the supply of planktonic food may play a role in that decoupling and limit subsequent recruitment (Carloni et al. 2018). The stronger correlation between *C. finmarchicus* and lobster postlarval abundance compared to the other zooplanktors (e.g. other copepod species, decapod larvae, gelatinous zooplankton, or chaetognaths) or abiotic factors (i.e. temperature, wind advection, and NAO index) indicated that *C. finmarchicus* abundance may be a limiting factor (Carloni et al. 2018). This



contention is further supported by an analysis of NOAA's EcoMon zooplankton data base spanning the entire GoM, where there was a strong correlation of the YOY index with *C. finmarchicus* and an associated assemblage of cold-water copepods (ASMFC 2020, Wahle et al. 2021). Here, we provide new evidence that the widening mismatch in phenology of larval lobster and *C. finmarchicus* may contribute to the downturn in lobster recruitment. We acknowledge that the long-term links we have reported could be driven by a larger ecosystem shift that we currently do not understand, which could be influencing both *Calanus* and postlarval lobsters in a similar fashion.

Region-wide sustained low levels of YOY lobster recruitment since 2012 have been of concern to the fishing industry, scientists, and fishery managers. Although adult lobster abundance remains at high levels, signs of a decline have emerged in recent years. The Coastwide Ventless Trap Survey and the Maine/New Hampshire Trawl Survey have also shown declines in sublegal lobster in coastal Maine with significant correlations to YOY indices (ASMFC 2020). This rate of decline in recruitment may be tempered to some degree by increased suitable thermal habitat in deep water and in the eastern GoM (Goode et al. 2019), although the agreement among several different depth-stratified surveys corroborates a declining population in the GoM. Additional research is required to reveal the mechanisms of the hypothesized trophic interaction between larval lobster and *Calanus*, but our 31-year time series reinforces our understanding of the linkages between American lobster recruitment and changes in the GoM's pelagic food web.

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## Author contributions

J.T.C., Conceptualization, data curation, formal analysis, methodology, writing-original draft, writing-review and editing. R.A.W., Conceptualization, funding acquisition, writing-original draft, writing-review and editing. D.M.F., Writing-original draft, writing-review and editing. P.G., Writing-review and editing. B.S., Writing-review and editing.

## Supplementary data

Supplementary data is available at the ICES Journal of Marine Science online.

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## Data availability

Data on lobster egg hatch were provided by New Hampshire Fish and Game Department and are available upon request. All other data from coastal New Hampshire were provided by a confidential third party and may be made available upon request with the permission of the third party.

## References

- Anger K, Storch V, Anger V, Capuzzo J.M. *Helgolander Meeresunters.* 1985;39:107–116.
- Annis ER, Incze LS, Wolff N et al. Estimates of *in situ* larval development time for the lobster, *Homarus americanus*. *J Crustac Biol* 2007;27:454–62 <https://doi.org/10.1651/S-2758.1>.
- Ascher JA. Climate change and an evolving fishery: do declining maternal size and planktonic foods affect lobster larval survival in the Gulf of Maine? *Ph.D. Dissertation*, University of Maine, 2023.
- ASMFC (Atlantic States Marine Fisheries Commission). Stock assessment report of the Atlantic States Marine Fisheries Commission. American lobster stock assessment for peer review. *ASMFC American Lobster Stock Assessment Subcommittee*, 2020.
- Bandara K, Varpe Ø, Wijewardene L et al. Two hundred years of zooplankton vertical migration research. *Biol Rev* 2021;96:1547–89. <https://doi.org/10.1111/brv.12715>.
- Baumgartner MF, Mate BR. Summertime foraging ecology of North Atlantic right whales. *Mar Ecol Prog Ser* 2003;264:123–35. <https://doi.org/10.3354/meps264123>.
- Beaugrand G, Brander KM, Lindley JA et al. Plankton effect on cod recruitment in the North Sea. *Nature* 2003;426:661–4. <https://doi.org/10.1038/nature02164>.
- Bigelow HB. *Plankton of the Offshore Waters of the Gulf of Maine*. 1926. Bulletin of the bureau of fisheries. Washington DC.
- Brander K. Impacts of climate change on fisheries. *J Mar Syst* 2010;79:389–402. <https://doi.org/10.1016/j.jmarsys.2008.12.015>.
- Burthe S, Daunt F, Butler A et al. Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. *Mar Ecol Prog Ser* 2012;454:119–33. <https://doi.org/10.3354/meps09520>.
- Campbell A, Stasko AB. Movement of lobsters (*Homarus americanus*) tagged in the Bay of Fundy, Canada. *Mar Biol.* 1986;92:393–404.
- Campbell A. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, eastern Canada. *Mar Biol.* 1986;92(3): 393–404.
- Carlioni JT, Goldstein J, Watson WH III. 2021. Movements of egg bearing American lobsters (*Homarus americanus*) during late-stage brooding and hatching. *Mar Ecol Prog Series.* 661:163–173.
- Carlioni JT, Wahle RA, Geoghegan P et al. Bridging the spawner-recruit disconnect: trends in American lobster recruitment linked to the pelagic food web. *Bull Mar Sci* 2018;94:719–35. <https://doi.org/10.5343/bms.2017.1150>.
- Carlioni JT, Watson WH. 2018. Distribution of ovigerous American lobsters near the Isles of Shoals, New Hampshire. *Bull Mar Sci* 94:555–570.
- Carlotti F, Hirche HJ. Growth and egg production of female *Calanus finmarchicus*: an individual-based physiological model and experimental validation. *Mar Ecol Prog Ser* 1997;149:91–104. <https://doi.org/10.3354/meps149091>.
- Cheung WWL, Watson R, Pauly D. Signature of ocean warming in global fisheries catch. *Nature* 2013;497:365–8. <https://doi.org/10.1038/nature12156>.

- Conover R. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia* 1988;167:127–42. <https://doi.org/10.1007/BF00026299>.
- Cooper R.A., Uzman J.R. Migrations and growth of deep-sea lobster, *Homarus americanus*. *Science* 1971;171:288–290.
- Cowan D.E., Watson W.H., Solow A.R., Mountcastle A.M.. 2007. Thermal histories of brooding lobsters, *Homarus americanus* in the Gulf of Maine. *Mar Biol.* 150:463–470.
- Cushing D.H. The regularity of the spawning season of some fishes. *J. Cons. Int. Explor.* 1969;33:81–92.
- Cushing DH. Plankton production and year class strength in fish populations: an update of the match/mismatch hypothesis. *Adv Mar Biol* 1990;26:249–93. [https://doi.org/10.1016/S0065-2881\(08\)60202-3](https://doi.org/10.1016/S0065-2881(08)60202-3).
- DeLorenzo Costa A, Durbin EG, Mayo CA. Variability in the nutritional value of the major copepods in Cape Cod Bay (Massachusetts, USA) with implications for right whales. *Mar Ecol* 2006;27:109–23. <https://doi.org/10.1111/j.1439-0485.2006.00087.x>.
- Doney SC, Ruckelshaus M, Duffy JE et al. Climate change impacts on marine ecosystems. *Ann Rev Mar Sci* 2012;4:11–37. <https://doi.org/10.1146/annurev-marine-041911-111611>.
- Durant JM, Hjermmann DO, Anker-Nilssen T et al. Timing and abundance as key mechanism affecting trophic interactions in variable environments. *Ecol Lett* 2005;8:952–8 <https://doi.org/10.1111/j.1461-0248.2005.00798.x>.
- Durant JM, Hjermmann DO, Ottersen G et al. Climate and match or mismatch between predator requirements and resource availability. *Clim Res* 2007;33:271–83. <https://doi.org/10.3354/cr033271>.
- Eagles MD, Aiken DE, Waddy SL. Influence of light and food on larval American lobsters, *Homarus americanus*. *Can J Fish Aquat Sci* 1986;43:2303–10. <https://doi.org/10.1139/f86-282>.
- Fields DM, Runge JA, Thompson CRS. A positive temperature-dependent effect of elevated CO<sub>2</sub> on growth and lipid accumulation in the planktonic copepod, *Calanus finmarchicus*. *Limnol Oceanogr* 2022;68:S87–S100. <https://doi.org/10.1002/lno.12261>.
- Free CM, Thorson JT, Pinsky ML et al. Impacts of historical warming on marine fisheries production. *Science* 2019;363:979–83. <https://doi.org/10.1126/science.aau1758>.
- Friedland KD, Morse RA, Shackell N, Tam JC, Morano JL, Moisan JR, Brady DC. Changing physical conditions and lower and upper trophic level responses on the US Northeast Shelf. *Front Mar Sci* 2020;7. <https://doi.org/10.3389/fmars.2020.567445>.
- Goldstein JS, Watson WH. Influence of natural inshore and offshore thermal regimes on egg development and time of hatch in American lobsters, *Homarus americanus*. *Biol Bull* 2015;228:1–12 <https://doi.org/10.1086/BBLv228n1p1>.
- González-Neto A, Langan JA, Palter JB. Changes in the Gulf Stream preceded rapid warming of the Northwest Atlantic Shelf. *Commun Earth Environ* 2021;2:74. <https://doi.org/10.1038/s43247-021-00143-5>.
- Goode A. *Anthropogenic impacts to essential habitats in the Gulf of Maine: a case study of the American lobster, Homarus americanus, and its fishery*. Ph.D. Dissertation, University of Maine, 2021.
- Goode AG, Brady DC, Steneck RS et al. The brighter side of climate change: how local oceanography amplified a lobster boom in the Gulf of Maine. *Global Change Biol* 2019;25:3906–17. <https://doi.org/10.1111/gcb.14778>.
- Haarr ML, Comeau M, Chassé J et al. Early spring egg hatching by the American lobster linked to rising water temperature in autumn. *ICES J Mar Sci* 2018.
- Haarr M.L., Miller E.H., Gaudette J., Rochette R. An assessment of the biological significance of a visual clutch staging scheme for ovigerous female american lobster (*Homarus americanus*). *Animals* 2023;13:3856. <https://doi.org/10.3390/ani13243856>.
- Häfker NS, Teschke M, Last KS et al. *Calanus finmarchicus* seasonal cycle and diapause in relation to gene expression, physiology, and endogenous clocks. *Limnol Oceanogr* 2018;63:2815–38. <https://doi.org/10.1002/lno.11011>.
- Harding GC, Drinkwater KF, Vass WP. Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Gulf of Maine: a new synthesis. *Can J Fish Aquat Sci*, 1983;40:168–84. <https://doi.org/10.1139/f83-027>.
- Harding GC, Pringle JD, Vass WP et al. Vertical distribution and daily movements of larval lobsters *Homarus americanus* over Browns Bank, Nova Scotia. *Mar Ecol Prog Ser* 1987;41:29–41. <https://doi.org/10.3354/meps041029>.
- Harvey M, Morrier G. Laboratory feeding experiments on zoea of northern shrimp *Pandalus borealis* fed with natural zooplankton. *Mar Ecol Prog Ser* 2003;265:165–74. <https://doi.org/10.3354/meps265165>.
- Heath MR, Boyle PR, Gislason A et al. Comparative ecology of overwintering *Calanus finmarchicus* in the northern North Atlantic, and implications for life-cycle patterns. *ICES J Mar Sci* 2004;61:698–708 <https://doi.org/10.1016/j.icesjms.2004.03.013>.
- Herrick FH. Natural history of the American lobster. *Bull Bur Fish* 1911;320-350.
- Herrick FH. The American lobster: a study of its habits and development. *Bull US Fish* 1895;15:1–252.
- Hirche H-J. Diapause in the marine copepod, *Calanus finmarchicus*—a review. *Ophelia* 1996;44:129–43. <https://doi.org/10.1080/00785326.1995.10429843>.
- Ji R, Runge JA, Davis CS et al. Drivers of variability of *Calanus finmarchicus* in the Gulf of Maine: roles of internal production and external exchange. *ICES J Mar Sci* 2022;79:775–84. <https://doi.org/10.1093/icesjms/fsab147>.
- Jonasdottir SH. Lipid content of *Calanus finmarchicus* during overwintering in the Faroe–Shetland Channel. *Fish Oceanogr* 1999;8 61–72. <https://doi.org/10.1046/j.1365-2419.1999.00003.x>.
- Junio MAR, Cobb JS. Natural diet and feeding habits of the postlarval lobster *Homarus americanus*. *Mar Ecol Prog Ser* 1992;85:83–91. <https://doi.org/10.3354/meps085083>.
- Jury S.H., Pugh T.L., Henninger H., Carloni J.T., Watson W.H. Patterns and possible causes of skewed sex ratios in American lobster. *Invertebrate Reproduction and Development*. 2019;63:189–199. <https://doi.org/10.1080/07924259.2019.1595184>.
- Kaartvedt S. Life history of *Calanus finmarchicus* in the Norwegian Sea in relation to planktivorous fish. *ICES J Mar Sci* 2000;57:1819–24. <https://doi.org/10.1006/jmsc.2000.0964>.
- Kane J. The feeding habits of co-occurring cod and haddock larvae from Georges Bank. *Mar Ecol Prog Ser* 1984;16:9–20 <https://doi.org/10.3354/meps016009>.
- Kann LM, Wishner K. Spatial and temporal patterns of zooplankton on baleen whale feeding grounds in the southern Gulf of Maine. *J Plankton Res* 1995;17:235–62. <https://doi.org/10.1093/plankt/17.2.235>.
- Katz C.H., Cobb J.S., Spaulding M. 1994. Larval behavior, hydrodynamic transport, and potential offshore to inshore recruitment in the American lobster *Homarus americanus*. *Marine Ecology Progress Series*. 103:265:273.
- Krouse J.S. 1973. Maturity, sex ratio and size composition of the natural population of American lobster, *Homarus americanus*, along the Maine coast. *Fish Bull.* 71(1):165–174.
- Layland EM. Ontogeny of size-specific prey selection and handling behavior of larval lobster (*Homarus americanus*). M.S. Thesis, University of Maine, 2023.
- Lee RF, Hagen W, Kattner G. Lipid storage in marine zooplankton. *Mar Ecol Prog Ser* 2006;307:273–306. <https://doi.org/10.3354/meps307273>.
- MacKenzie BR. Assessment of temperature effects on interrelationships between stage durations, mortality, and growth in laboratory reared *Homarus americanus* Milne Edwards larvae. *J Exp Mar Biol Ecol* 1988;116:87–98 [https://doi.org/10.1016/0022-0981\(88\)90248-1](https://doi.org/10.1016/0022-0981(88)90248-1).
- Meise CJ, O'Reilly JE. Spatial and seasonal patterns in abundance and age-composition of *Calanus Finmarchicus* in the Gulf of Maine and

- on Georges Bank: 1977–1987. *Deep Sea Res Part II* 1996;43:1473–501. [https://doi.org/10.1016/S0967-0645\(96\)00048-3](https://doi.org/10.1016/S0967-0645(96)00048-3).
- Melle W, Runge J, Head E *et al.* The North Atlantic Ocean as habitat for *Calanus finmarchicus*: environmental factors and life history traits. *Prog Oceanogr* 2014;129:244–84. <https://doi.org/10.1016/j.pocean.2014.04.026>.
- Mertz G, Myers RA. Match/mismatch predictions of spawning duration versus recruitment variability. *Fish Oceanogr* 1994;3:236–45. <https://doi.org/10.1111/j.1365-2419.1994.tb00101.x>.
- Meyer-Gutbrod EL, Greene CH, Davies KTA *et al.* Ocean regime shift is driving collapse of the North Atlantic right whale population. *Oceanography* 2021;34:22–31. <https://doi.org/10.5670/oceanog.2021.308>.
- Mills KE, Pershing AJ, Brown CJ *et al.* Fisheries management in a changing climate. *Oceanography* 2013;26:191–5.
- Mullin MM. Comparative ecology of the genus *Calanus* in the Gulf of Maine. Ph.D. Thesis, Department of Biology, Harvard University, 1963.
- Nye JA. State of the Gulf of Maine Report: Climate Change and Its Effects on Ecosystems, Habitats and Biota. Gulf of Maine Council on the Marine Environment, 2010. <http://www.gulfofmaine.org/2/wp-content/uploads/2014/03/climate-change-and-its-effects-on-ecosystems-habitats-and-biota.pdf>. accessed 3/1/2024.
- Oviatt CA. The changing ecology of temperate coastal waters during a warming trend. *Estuaries*, 2004;27:895–904. <https://doi.org/10.1007/BF02803416>.
- Pepin P, Head EJH. Seasonal and depth-dependent variations in the size and lipid contents of stage 5 copepodites of *Calanus finmarchicus* in the waters of the Newfoundland shelf and the Labrador sea. *Deep Sea Research Part I Oceanogr Res Pap* 2009;56:989–1002.
- Perretti CT, Fogarty MJ, Friedland KD *et al.* Regime shifts in fish recruitment on the Northeast US Continental Shelf. *Mar Ecol Prog Ser* 2017;574:1–11. <https://doi.org/10.3354/meps12183>.
- Pershing AJ, Alexander MA, Nernandez CM *et al.* Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 2015;350:809–12. <https://doi.org/10.1126/science.aac9819>.
- Pershing AJ, Griffis RB, Jewett EB *et al.* Oceans and marine resources. In: Reidmiller DR, Avery CW, Easterling DR *et al.* (eds). *Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment*, Vol. II. Washington, DC: US Global Change Research Program, 2018, 353–90.
- Pershing AJ, Alexander MA, Brady DC, Brickman D, Curchitser EN, Diamond AW, McClenachan L, Mills KE, Nichols OC, Pendleton DE, Record NR, Scott JD, Staudinger MD, 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 Anthropocene* : <https://doi.org/10.1525/elementa.2020.00076>.
- Pinsky ML, Mantua JM. Emerging adaptation approaches for climate-ready fisheries management. *Oceanography* 2014;27:146–59 <https://doi.org/10.5670/oceanog.2014.93>.
- Planque B, Batten SD. *Calanus finmarchicus* in the North Atlantic: the year of *Calanus* in the context of interdecadal change. *ICES J Mar Sci* 2000;57:1528–35. <https://doi.org/10.1006/jmsc.2000.0970>.
- Poloczanska ES, Burrows MT, Brown CJ *et al.* Responses of marine organisms to climate change across oceans. *Front Mar Sci* 2016;3:1–21. <https://doi.org/10.3389/fmars.2016.00062>.
- Record NR, Balch WM, Stamieszkin K. Century-scale changes in phytoplankton phenology in the Gulf of Maine. *PeerJ* 2019;7:e6735. <https://doi.org/10.7717/peerj.6735>.
- Richards RA, Hunter M. Northern shrimp *Pandalus borealis* population collapse linked to climate-driven shifts in predator distribution. *PLoS One* 2021;16:e0253914. <https://doi.org/10.1371/journal.pone.0253914>.
- Richards RA, O'Reilly JE, Hyde KJW. Use of satellite data to identify critical periods for early life survival of northern shrimp in the Gulf of Maine. *Fish Oceanogr* 2016;25:306–19 <https://doi.org/10.1111/fog.12153>.
- Richards RA. Phenological shifts in hatch timing of northern shrimp *Pandalus borealis*. *Mar Ecol Prog Ser* 2012;456:149–58. <https://doi.org/10.3354/meps09717>.
- Runge JA, Ji R, Thompson CRS *et al.* Persistence of *Calanus finmarchicus* in the western Gulf of Maine during recent extreme warming. *J Plankton Res* 2015;37:221–32. <https://doi.org/10.1093/plankt/fbu098>.
- Skottene E, Tarrant AM, Olsen AJ *et al.* The  $\beta$ -oxidation pathway is downregulated during diapause termination in *Calanus* copepods. *Sci Rep* 2019;9:166–86.
- Staudinger MD, Mills KE, Stamieszkin K *et al.* It's about time: a synthesis of changing phenology in the Gulf of Maine ecosystem. *Fish Oceanogr* 2019;28:532–66. <https://doi.org/10.1111/fog.12429>.
- Templeman W. The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster. *J Biol Board Canada* 1936;2:485–97. <https://doi.org/10.1139/f36-029>.
- Townsend DW, Pettigrew NR, Thomas MA *et al.* Warming waters of the Gulf of Maine: the role of shelf, slope and Gulf Stream Water masses. 2023;215:103030. <https://doi.org/10.1016/j.pocean.2023.103030>.
- Varpe Ø, Fiksen Ø. Seasonal plankton–fish interactions: light regime, prey phenology, and herring foraging. *Ecology* 2010;91:311–8. <https://doi.org/10.1890/08-1817.1>.
- Wahle RA, Carloni J, Shank B *et al.* Bridging the spawner–recruit disconnect II: revealing basin–scale correlations and phenology shifts between zooplankton and lobster settlement dynamics in the Gulf of Maine. *Final project report*. Maine Department of Marine Resources Lobster Research Collaborative, 2021.
- Waller JD, Reardon KM, Caron SE *et al.* A comparison of size at maturity of female American lobsters (*Homarus americanus*) over three decades and across coastal areas of the Gulf of Maine using ovarian staging. *ICES J Mar Sci* 2021;78:1267–77.
- Waller JD, Reardon KM, Caron SE *et al.* Decrease in size at maturity of female American lobsters (*Homarus americanus*) over a 50-year period in Maine, USA. *J Crustac Biol* 2019;39:509–15 <https://doi.org/10.1093/jcbl/ruz021>.
- Williams R. Spatial heterogeneity and niche differentiation in oceanic zooplankton. *Hydrobiologia* 1988;167–8:151–9. <https://doi.org/10.1007/BF00026301>.
- Woodley TH, Gaskin DE. Environmental characteristics of North Atlantic right and fin whale habitat in the lower Bay of Fundy. *Can J Zool* 1996;74:75–84. <https://doi.org/10.1139/z96-010>.

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