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Basin-Scale Coherence in Phenology of Shrimps and Phytoplankton in the North Atlantic Ocean

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Climate change could lead to mismatches between the reproductive cycles of marine organisms and their planktonic food. We tested this hypothesis by comparing shrimp (*Pandalus borealis*) egg hatching times and satellite-derived phytoplankton bloom dynamics throughout the North Atlantic. At large spatial and long temporal (10 years or longer) scales, hatching was correlated with the timing of the spring phytoplankton bloom. Annual egg development and hatching times were determined locally by bottom water temperature. We conclude that different populations of *P. borealis* have adapted to local temperatures and bloom timing, matching egg hatching to food availability under average conditions. This strategy is vulnerable to interannual oceanographic variability and long-term climatic changes.

During the early 1990s, populations of the northern shrimp (*Pandalus borealis*) increased to levels previously unobserved in the North Atlantic, resulting in the expansion of existing fisheries and the establishment of new ones (fig. S1). The shrimp population increases have been attributed to concurrent decreases in groundfish predators and to large-scale climatic changes (1–8). A link between spring sea surface temperatures (SSTs) and shrimp larval survival has been reported in the Gulf of St. Lawrence and the Gulf of Maine (4, 9). Because SSTs also influence the onset and intensity of the spring phytoplankton bloom (10), the success of the shrimp hatch may be linked to the spring bloom. Until recently, we lacked the tools necessary to study the matter on a globally significant scale (11, 12). We tested Cushing's hypothesis (13), that variability in year-class strength is at least partly due to matches or mismatches in the timings of larval release and the spring phytoplankton bloom, by comparing shrimp hatch dates and spring bloom timing at the scale of the North Atlantic basin. Specifically, we asked whether there is evidence that *P. borealis* has adapted its reproductive

cycle to match hatching times with seasonal phytoplankton dynamics in different ecological regimes throughout its wide latitudinal range (42° to 80°N).

Characteristics of the spring bloom, particularly its timing, vary with latitude (14). It follows that if shrimp are to match hatch and bloom timing over a broad latitudinal band, there must be some local genetic or behavioral adaptation of their annual reproductive cycles. Furthermore, shrimp must adapt to local differences in bottom water temperatures, which are known to determine the duration of the summer-to-spring egg-bearing (development) period (6, 15–17), and hence egg hatching times. Short-term oceanographic variability or long-term climatic changes might degrade the relationship between hatch and bloom (fig. S2).

We found average bottom temperatures correlated with the length of the egg development period throughout the North Atlantic Ocean

(Fig. 1) (18). Two southern stocks (Gulf of Maine and Gulf of St. Lawrence) experienced the warmest temperatures (~6° and 5°C, respectively) and had the shortest egg development periods (~6 and 7 months), whereas two northern stocks (Northern Iceland and Svalbard) living at the coldest temperatures (~1° and 1.5°C) had the longest development periods (~10 and 19 months). Despite development times ranging between 6 and 10 months and spawning times differing by ≤3 months, in 6 of the 13 areas the mean times for 50% hatching and maximum chlorophyll concentrations differed by only a few days (Fig. 2A). Mean hatch and bloom initiation times for all stocks in the North Atlantic differed by less than a week. The timing of phytoplankton bloom and hatch north of 60°N are earlier than would be predicted by latitude alone, probably in part because of the strong influence of the annual melting of sea ice (19).

When hatching, bloom maximum, and spawning times were regressed separately against latitude, the third-order polynomial fits for hatching and bloom times were both significant and identical in shape (Fig. 2B). However, the regression between spawning times and latitude did not show a latitudinal pattern (fig. S3). Because the duration of the egg development period is dependent on bottom temperature, which has little influence on the timing of phytoplankton blooms, spawning times must have evolved according to local temperatures to make hatch and bloom times coincide.

Data from the Newfoundland shelf confirm that later hatchings are a direct result of longer egg development times (Fig. 3A). Because water temperatures determine the duration of the egg development period (Fig. 1), they also determine hatching times (Fig. 3B). During the early 1990s, when water temperatures were colder, egg hatching was later (Fig. 3C) and the Newfoundland stock increased markedly, as shown by the catch per unit of effort from commercial trawlers (Fig. 3D).

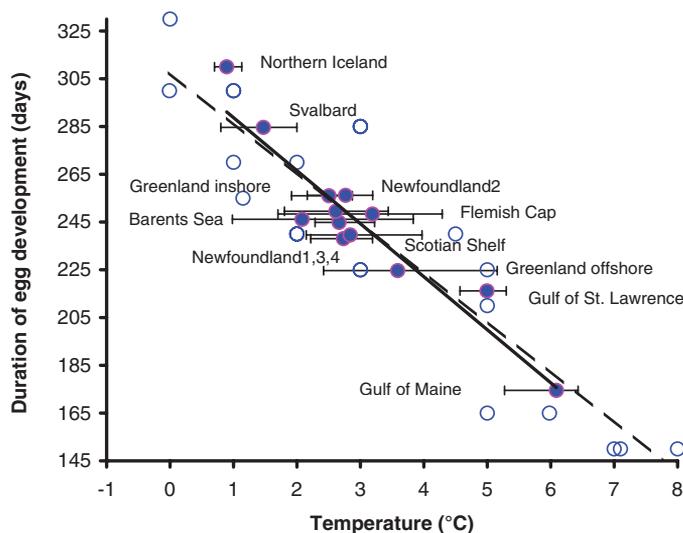


Fig. 1. Mean length of the egg-bearing (development) period versus ambient bottom temperatures in different areas. Solid circles and the solid regression line indicate data from this study; areas are identified. Bars show the range of annual mean temperatures for each shrimp survey data series. Open circles and dashed regression line indicate published data (6). Both regression lines from these independent studies are significant ($P < 0.01$), but they are not significantly different from each other.

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These results argue for the evolution of *P. borealis* egg hatch timing to accommodate to long-term average bottom temperatures and bloom times in each area, rather than for a direct link between egg hatching and spring blooms mediated by, for example, a chemical cue from

senescent bloom material arriving at the ocean bottom. They also indicate that the population increases observed throughout much of the northwest Atlantic in the early 1990s were partly a result of later egg hatching times due to the widespread colder bottom water temper-

atures during this period, caused by changes in Arctic climate that resulted in the propagation of anomalously cold low-salinity waters down the western North Atlantic (fig. S1) (8, 20). In following years, bottom water temperature increases triggered earlier hatching relative to

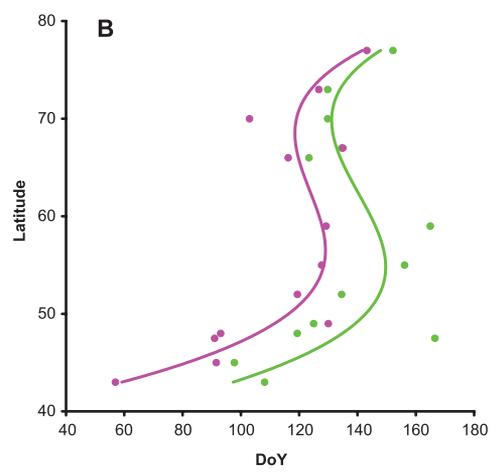
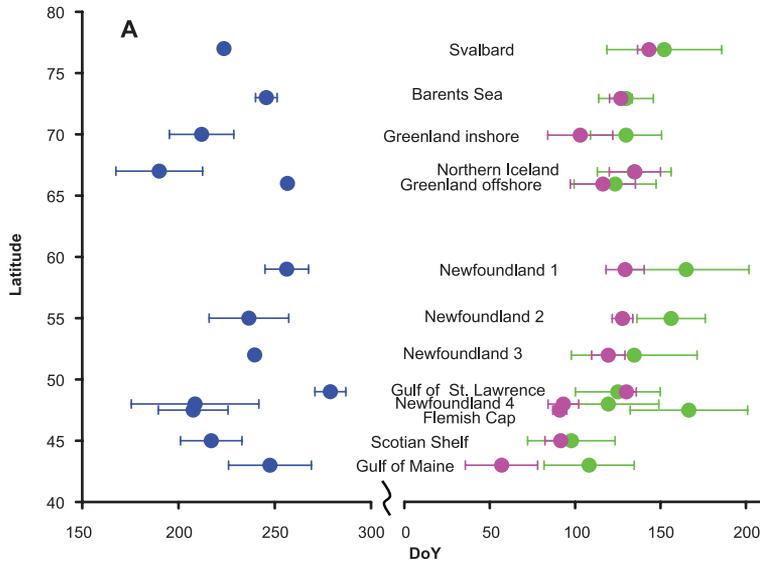
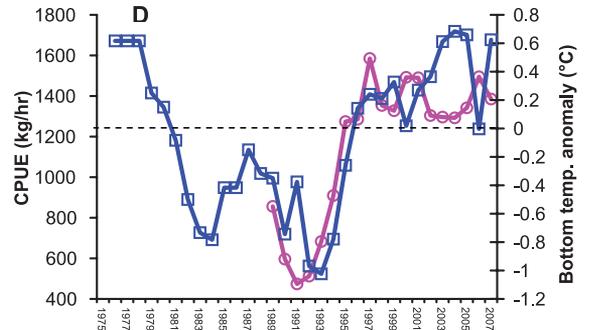
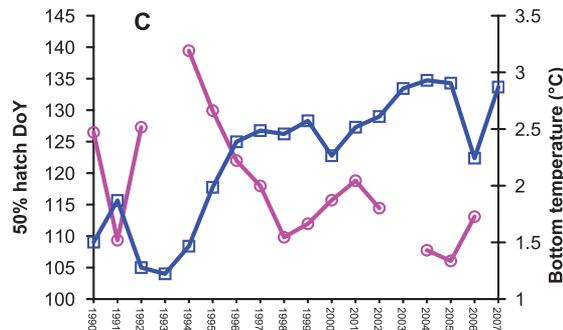
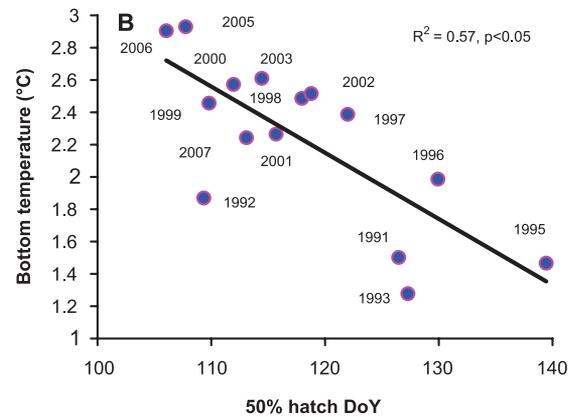
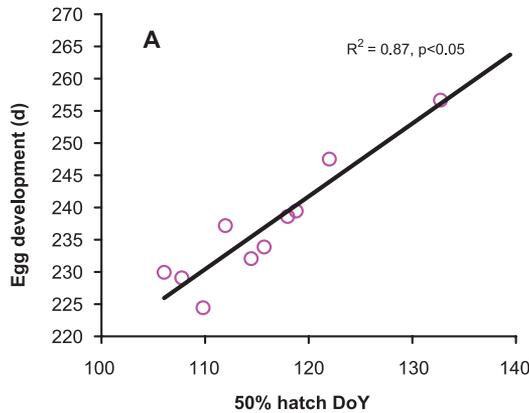


Fig. 2. Phenology of shrimp and phytoplankton as a function of latitude. **(A)** Days of the year (DoY) for mean shrimp spawning (blue circles) and hatch (pink circles) times at 50% completion (± 1 SD) and mean timing of peak chlorophyll

concentration (green circles). Bars indicate mean bloom initiation and completion times for each of the stock areas or subareas. Eggs are spawned in the summer/fall and are carried while they develop on the abdomen for 6 to 10 months until they hatch in the spring. **(B)** Third-order polynomial fits of 50% hatch DoY (pink line, $R^2 = 0.81$, $P < 0.01$) and phytoplankton bloom maximum (green line, $R^2 = 0.47$, $P < 0.05$) regressed against latitude as the independent variable. The fit between latitude and spawn timing ($R^2 = 0.04$) is not significant (fig. S3). A linear regression between hatch and bloom timing is significant at $P < 0.01$.

Fig. 3. Local influences on egg hatching times and population changes on the south Newfoundland Shelf. **(A)** Length of egg development from year y to $y + 1$ versus 50% hatching DoY in year $y + 1$. **(B)** Annual mean bottom temperatures measured in the fall of year y versus 50% hatching DoY in year $y + 1$. **(C)** Annual changes in 50% hatch DoY (pink circles) and bottom temperatures (blue squares) during and after the period of increasing abundances. **(D)** Bottom temperature anomalies (blue squares) and catch per unit of effort from commercial shrimp trawlers (pink circles). Survey bottom temperatures were not available before 1991; representative deep water (150 m) temperatures on Hamilton Bank were used for this period. Commercial shrimp trawls mainly catch larger, older (≥ 4 years) shrimp, hence increased larval survival would be reflected in data on catch per unit of effort only after several years.



the spring bloom and surface warming, resulting in less-frequent strong year classes. Shrimp abundance, however, remained high because of continued low predation pressure from depleted groundfish stocks.

The Gulf of St. Lawrence has the lowest annual minimum SSTs, and the bloom begins at relatively cool SSTs as compared with those in other areas, but its SSTs warm up most rapidly (Fig. 4). More rapid warming results in warmer SSTs during the phytoplankton bloom when food is most abundant, enhancing larval growth and survival. This explains the observed positive correlation between SST warming rates and larval survival (9). The longstanding but contradictory negative relationship between coastal spring SSTs measured at Boothbay Harbor, Maine, and larval survival reported in the Gulf of Maine (4, 15), is likely to be a result of the Gulf of Maine's location at the southern end of the range of *P. borealis*, where both SSTs and bottom temperatures are warm. High bottom temperatures in the Gulf of Maine (Fig. 1) result in the earliest hatching dates and a long time lag between hatch and bloom (Figs. 2A and 4). It is also the only stock in which egg-bearing females migrate during winter from offshore waters into shallow, colder nearshore water (4, 15). This migration may be a behavioral adaptation to warm bottom water temperatures that delays egg development and brings hatching closer to the spring bloom. This effect would be enhanced when coastal SSTs in Boothbay Harbor (representative of the well-mixed nearshore waters sought by egg-bearing females) were colder, leading to the observed negative correlation. The later bloom at Flemish Cap is probably a result of the oceanographic conditions prevailing at the front between the Labrador and North Atlantic Currents. It appears that the shrimp population at Flemish Cap established itself only recently through larval drift from the adjacent south Newfoundland shelf (21). The large off-

set in hatch and bloom timing at Flemish Cap (Figs. 2 and 4) may occur because the determinants of hatch timing have evolved under different conditions.

Decoupling a match between hatching and bloom to long-term average environmental conditions may arise if the interacting environmental factors are driven by different oceanographic processes; that is, for *P. borealis*, bottom temperatures determine egg development and hatch times (Fig. 1), and surface temperatures (Fig. 4) influence the timing of the spring bloom and larval growth rates. Specific conditions leading to a match or mismatch may differ between areas with different magnitudes of, and temporal relationships between, the factors associated with larval survival, as in the examples above for the Gulf of Maine, the Gulf of St. Lawrence, and Flemish Cap (Figs. 1 and 4). The collapse of the Gulf of Maine shrimp stock in the 1970s has been attributed to warmer temperatures or overfishing (4). More likely, both contributed. Further elucidation of area-specific recruitment mechanisms will help the development of management models that incorporate the important environmental factors influencing stock productivity. The confounding effects of top-down processes such as trophic cascades (7) further complicate this difficult task.

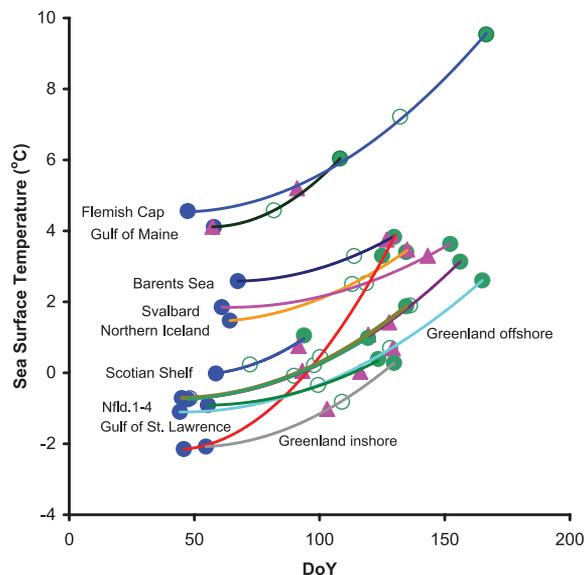
Our macroecological approach using satellite-sensed data has demonstrated the evolutionary plasticity of an important marine species adapting to distinct environmental conditions across its range and provides a framework for discussion of how shrimp stocks and possibly other economically and ecologically important species might respond to climate change. In the climate change context, we may anticipate that *P. borealis* will be affected by changes in both the timing of the spring bloom and bottom temperatures. A tendency to early stratification (for example, caused by increased melting of

ice or faster warming of surface waters), which would favor early blooms, may be offset by higher winds (a higher frequency of storms). Furthermore, bottom temperatures are affected by quite different processes. Our understanding of how climate change may affect these processes is improving, but accurate prediction of how they in turn will affect living marine resources will require continued building of relevant environmental time series and further model studies that elucidate the coupling between the physics and biology of the oceans.

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22. This analysis was made possible by the satellite data provided by NASA and the efforts of the technical personnel in six countries whose efforts at sea and in the laboratory provided the biological and physical oceanographic data. We also thank G. White III for extensive data preparation. This work was supported by the Canadian Space Agency through the Government Related Initiatives Program and by the Natural Sciences and Engineering Research Council of Canada through research grants to T.P. and S.S. This work is a contribution to the National Centre for Earth Observation and the Oceans 2025 programs of the Natural Environment Research Council of the UK.

Fig. 4. SSTs for each study area at their annual minimum (solid blue circles), at phytoplankton bloom initiation (open green circles), at peak chlorophyll concentration (solid green circles), and at 50% hatch times (pink triangles).



Supporting Online Material

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Materials and Methods
Figs. S1 to S6
Table S1
References

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