Trends in the Reproductive Phenology & Thermal Sensitivity of Thirteen Populations of Small Pelagic Fishes across North American Waters

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1. Abstract

The seasonal timing when small pelagic fishes (SPF) reproduce can influence recruitment via synchrony with plankton blooms. Multiple studies have shown the seasonality of SPF reproduction is shifting under climate change, but no global synthesis has assessed variations by species, ocean basins, or latitude. As part of a PICES/ICES Working Group on Sustainable Pelagic Forage Communities (WGSPF), 59 times series were identified for synthesis. These time series represent 24 species from 28 ecoregions with data from ichthyoplankton and spawning migration surveys, maturity stages and gonadal development, otolith estimation of hatch dates, and historical documentation of spawning runs. Open-source code is being developed to analyze weekly-to-annual time series uniformly. An initial analysis demonstrates our approach using seven species from both coasts of North America. We detected a trend for summer/fall spawning species to reproduce later and spring spawners to reproduce earlier, with some exceptions. For nine out of thirteen populations, the phenological signal-to-noise ratio exceeded one, indicating long-term climate trends have a greater influence on spawning time than interannual variability. No distinct latitudinal trends were identified, but species-specific patterns were detected. Sardine and sand lance often displayed larger variations in phenology than co-occurring species. Despite rapid warming in the Northeast United States, its SPF populations exhibited low phenological sensitivity to temperature. Consequently, we identified a statistically significant, inverse relationship between rates of warming and thermal sensitivity of reproductive timing. The inverse relationship suggests that SPF could have a high adaptive capacity to handle changes in temperature without falling victim to phenological mismatches.

2. Introduction

- Small pelagic fish (SPF), such as sardine, anchovy, and herring, comprise >30% of global capture fisheries.
- They play a prominent role in fisheries for human consumption, fish meal and oil, and agricultural and aquacultural feed. SPF connect multiple trophic levels serving as a key prey item for squid, predatory fishes, seabirds, and marine mammals.
- SPF are sensitive to climate variability and climate change and are known to undergo dramatic boom-bust cycles in abundance and recruitment productivity.
- Many boom-bust cycles have occurred somewhat synchronously across ecosystems due to teleconnections.
- Changes in reproductive timing (i.e., phenology) have been documented in many SPF due to climate change, but a cross-region and cross-species synthesis has not been previously undertaken.
- A Joint ICES/PICES Working Group on Sustainable Pelagic Forage Communities (WGSPF) provides an opportunity to undertake this type of global synthesis.

Research Objectives:

1. Quantify interannual variability and long-term trends in SPF spawning phenology, with the goal of assessing the observed signal-to-noise ratio
2. Determine if regions with more rapid temperature changes are associated with faster shifts in phenology
3. Compare results across regions, species, and latitudinal gradients

3. Methods Overview

- **59 time series** suitable for analysis of SPF reproductive phenology were identified by WGSPF **(Figure 1).** A subset of 13 time series from North America were selected to test methods **(Table 1).**
- **Challenge:** Data from many fisheries-independent surveys are accessible to WGSPF members, but raw data cannot be shared internationally.
- **Solution:** Code templates developed to analyze time series in a uniform way without the need for data sharing. These will be available in Matlab and R.
  - → Separate templates for annual, monthly, and weekly time series **(Figure 2).**
  - → Minimal data requirements – only data on a spawning indicator (e.g., larval abundance, gonado-somatic index), temperature, and date are needed
  - → HadISST used to fill temperature data gaps
  - → A "rotated year" allows for analysis of diverse spawning seasons
  - → **Local experts still need to make key decisions** about temporal binning and partitioning of data by stock, age class, sex, fishing gear, etc.
- **Phenology metrics calculated:** Seasonal center of gravity, season start, midpoint, end, and duration
- **Trend detection** based on linear regression; assessment of interannual variability based on standard deviation (S.D.) of detrended data; signal-to-noise = trend/S.D.; thermal sensitivity based on regression between phenology metrics and temperature time series

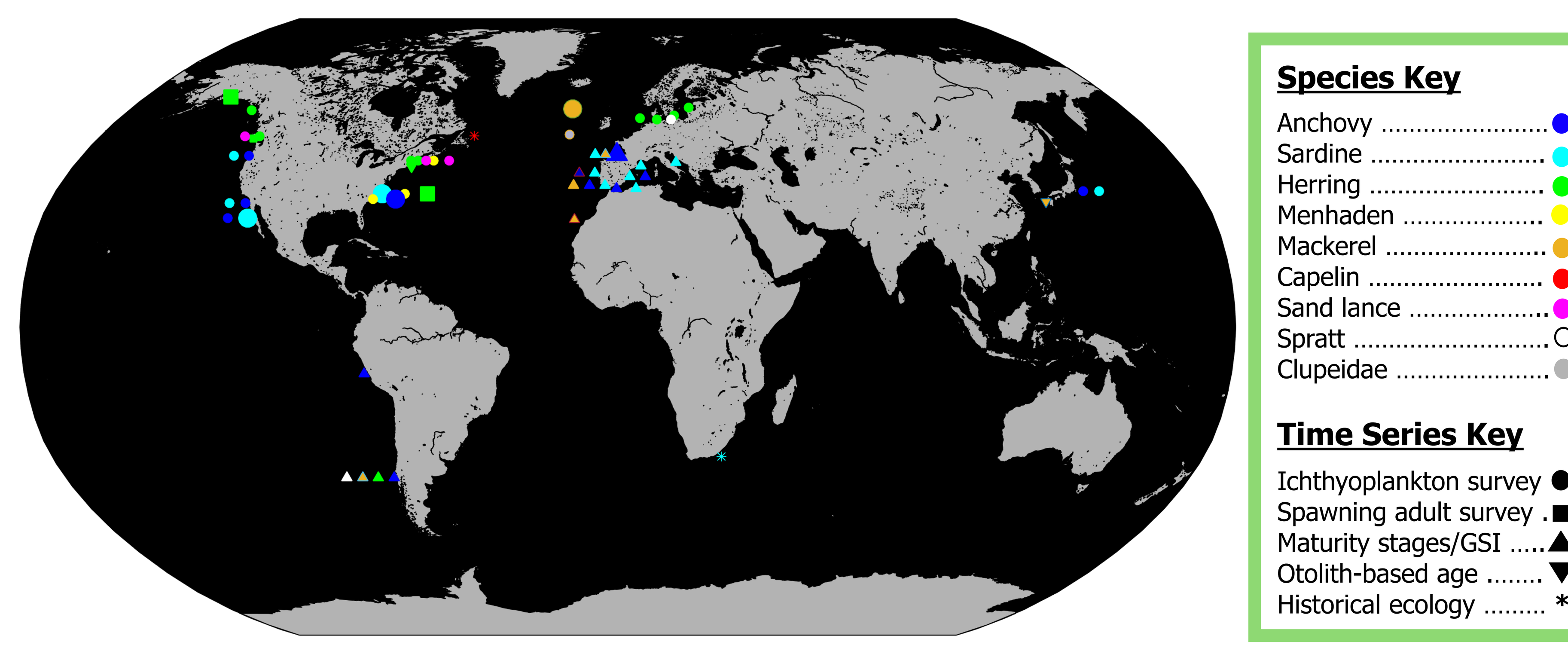


Figure 1. SPF time series suitable for analysis of reproductive phenology. Locations are approximate and markers from same time series are offset for visibility. Larger markers indicate a time series that examines two species per category, two stocks, or two phenophases.

Time Series Number	Sampling Program Name	Species	Spawning Season	Sampling Frequency	Binning	Years Analyzed
1	DFO - British Columbia	Sand lance	Spring	Quasi-monthly	5-year	1978-2013
2		Pacific herring	Spring			
3	Newport Line, Oregon	Northern anchovy	Spring/ Summer	Biweekly, but analyzed with monthly code template	1-year	1996-2022
4		Pacific sardine	Spring/ Summer			
5	CalCOFI	Northern anchovy	Spring	Monthly	10-year	1951-2015
6		Pacific sardine	Spring			
7	IMECOCAL	Northern anchovy	Spring	Monthly	10-year	1951-2019
8		Pacific sardine (spring phenophase)	Spring			
9		Pacific sardine (fall phenophase)	Late Summer/Fall			
10	DFO - Newfoundland	Capelin	Summer	Annual	Binning by NAFO divisions	1920-2020
11	EcoMon - Northeast US	Sand lance	Winter/Early Spring	Quasi-monthly	5-year	1999-2019
12		Atlantic herring	Fall			
13	Bridgenet - Beaufort Inlet, North Carolina	Atlantic menhaden	Winter/ Spring	Weekly	1-year	1987-2019

Table 1. Characteristics of 13 time series used in North American trial analysis. Sampling frequency refers to the sampling interval used in this analysis, which can differ from a time series' native sampling frequency if several years are binned together.

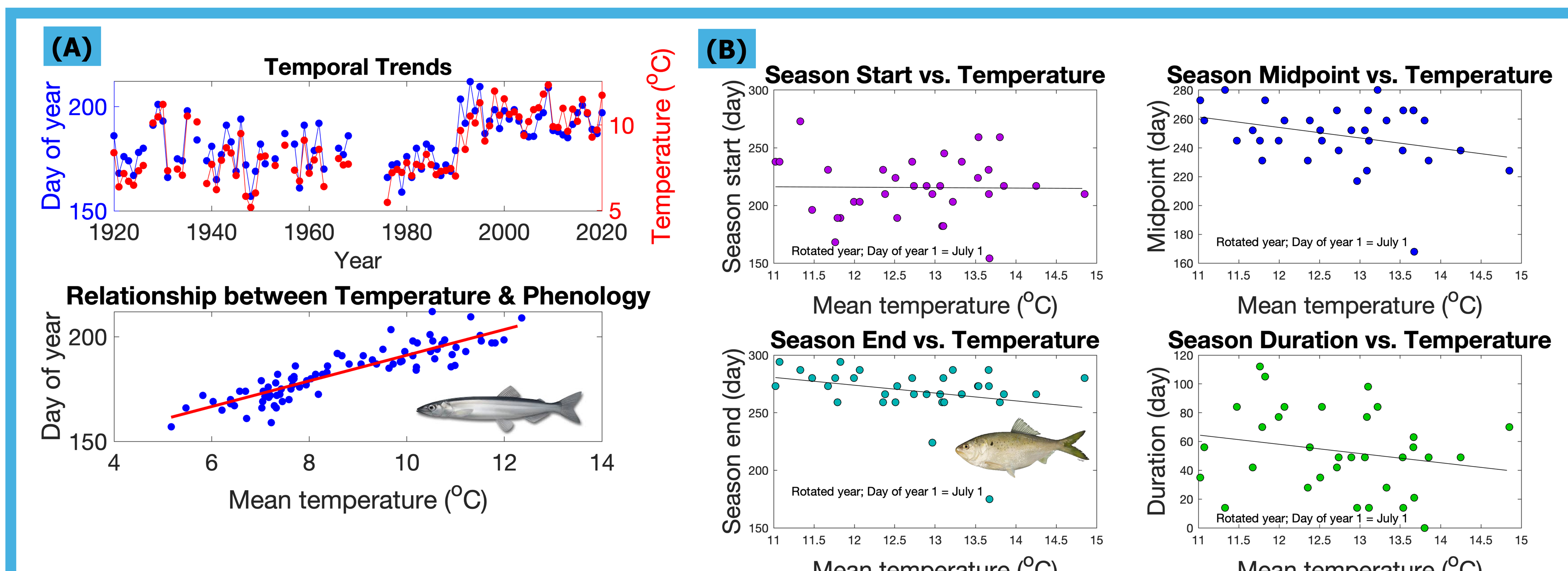
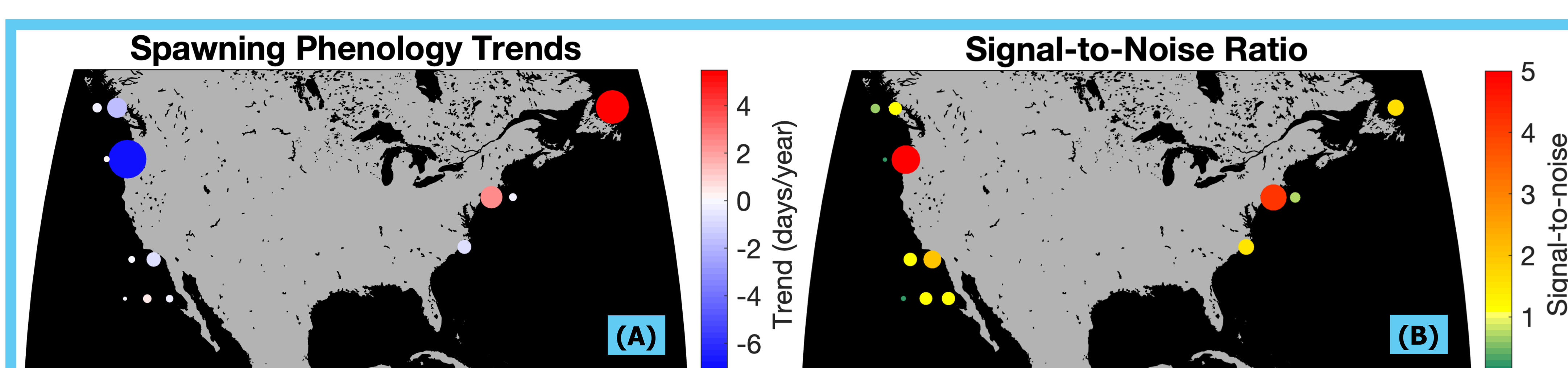


Figure 2. Example output from code templates. (A) Annual time series example – Capelin from Newfoundland. (B) Weekly time series example – Atlantic menhaden from Beaufort, North Carolina.



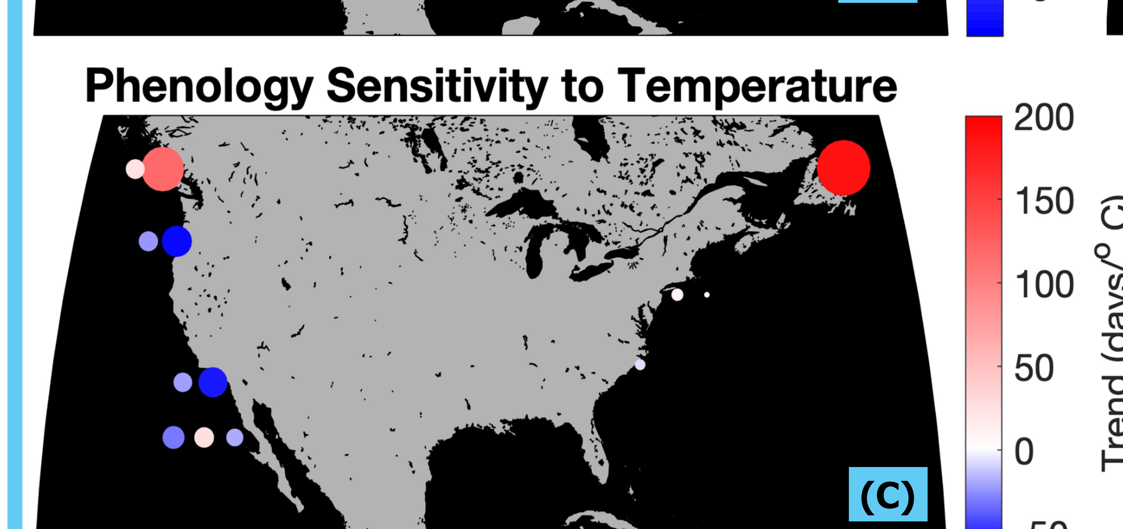


Figure 3. Spatial patterns related to reproductive phenology across 13 North American SPF time series. (A) Long-term trends in spawning phenology; (B) Signal-to-noise ratios assessing the influence of long-term trends relative to interannual-to-decadal variability in phenology. Values > 1 indicate a dominance of long-term trends; (C) Phenological sensitivity to temperature based on the slope of linear regressions between spawning phenology and local temperature.

4. Results and Discussion

- Most time series identified as suitable for analysis of SPF reproductive phenology are from **Europe and North America (Figure 1).**
- Spring spawning stocks had trends towards **earlier reproduction,** whereas summer and falling spawning fishes experienced **delayed phenology (Figure 2A).**
- Despite high interannual variability in abundance that leads to boom-bust cycles among SPF fisheries, **trends in phenology were larger than interannual variability** in 69% of the time series **(Figure 2B).**
- Low phenological sensitivity to temperature occurred in the **Northeast US.** This is surprising since this is one of the most rapidly warming ecosystems **(Figure 2C).**
- This resulted in **a significant, inverse relationship** between temperature trends and SPF thermal sensitivity **(Figure 4).** This could be due to rapid adaptation to changing conditions that could possibly guard against seasonal, trophic mismatches.
- **Latitudinal trends** in phenology were marginally insignificant (R^2 = 0.25, p = 0.0814, d.f. = 11). This seems to reflect high interspecific variability in phenological trends within each region.
- Among **co-occurring species,** sand lance exhibits faster phenology trends, a greater signal-to-noise ratio, and higher thermal phenological sensitivity than herrings. Sardine exhibited more rapid trends and a greater signal-to-noise ratio than anchovy.
- Analysis of phenology time series from **additional regions** will help to determine the robustness of initial results.

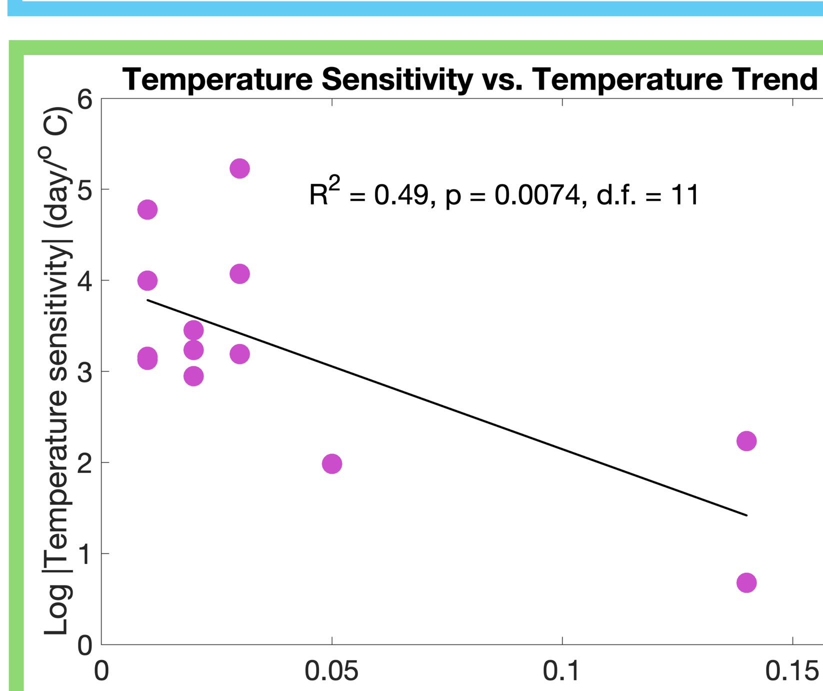


Figure 4. Temperature trends at each location vs. the sensitivity of SPF reproductive phenology to temperature variations.

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