

## **Draft Working Paper**

### **Ecosystem and Climate Influences on Stock Dynamics of Atlantic Bluefin Tuna (BFT)**

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#### **Overview**

This review of scientific literature was completed to characterize the published work related to the ecosystem and climate influences on stock dynamics of Atlantic Bluefin Tuna (BFT). This collection of relevant literature will provide a reference document for environmental considerations for future modeling work. Literature concerning both the east and west stocks of Atlantic bluefin tuna, as well as some relevant literature concerning Pacific bluefin tuna, have been included.

#### **Background**

Atlantic bluefin tuna (*Thunnus thynnus*) are a large, highly migratory, and endothermic species, subject to important fisheries throughout their range in the Atlantic (Bigelow and Schroeder 1953, Dickson and Graham 2004, Block et al. 2005, Fromentin and Powers 2005, Kerr et al. 2017). Many different climate and oceanographic factors influence the stock dynamics of Atlantic bluefin tuna (e.g., Humston, et al. 2000, García et al. 2013, Golet et al. 2013, Fromentin et al. 2014, Hansell et al. 2020, Malca et al. 2022). Despite their (limited) endothermy, bluefin tuna are subject to the influences of water temperature both intrinsically (e.g., larval growth rates, Reglero et al. 2018) and extrinsically (e.g., prey distribution shifts, MacKenzie et al. 2014). Atlantic bluefin tuna as managed by ICCAT as two stocks: east (Mediterranean spawning) and west (Gulf of Mexico spawning) (Anon. 2017, Anon. 2021), although there is evidence of spawning activity occurring in the Slope Sea off the Mid Atlantic Bight (Richardson et al. 2016a, Richardson et al. 2016b, Hernandez et al. 2022). There is evidence for a high degree of natal homing, as well as extensive stock mixing (Lutcavage et al. 1999, Block et al. 2005, Rooker et al. 2008a, Rooker et al. 2008b, Dickhut et al., 2009, Galuardi et al. 2010, Rodríguez-Ezpeleta et al. 2019, Kerr et al. 2020).

The relatively discrete regional spawning and oceanic-scale feeding habitats of Atlantic bluefin tuna are experiencing the impacts of climate change. The conventional spawning location of the western stock, the Gulf of Mexico, has been warming both at the surface and at depth, and acidification is occurring (Ochoa et al. 2021, Lawman et al. 2022), which could lead to large ecosystem changes including population productivity of fishes (Trifonova et al. 2019). Changing dynamics of the Gulf Stream, Labrador Current, and gyres have caused changes in fisheries and ecosystems in the North Atlantic (Nye et al. 2010, Oviatt et al. 2015, Pershing et al. 2015, Brickman et al. 2021, Neto et al. 2021). The Mediterranean Sea, the spawning area of the eastern stock, has also been experiencing warming and ecosystem change (Moulec et al. 2019, Pastor et al. 2020).

## **Ecosystem Influences on Distribution and Habitat Use**

Water temperature affects all life history stages of bluefin tuna, whether directly or indirectly, from spawning (Baglin 1982, Karakulak et al. 2004, Rooker et al. 2007), to larval mortality (Pacific bluefin; Kimura et al. 2010), to juvenile growth rates (García et al. 2013, Galuardi and Lutcavage 2012), to adult migrations and foraging ecology (Humston et al. 2000, Fromentin and Fonteneau 2001). Although other variables are investigated, most studies focus on temperature. Bluefin occupy pelagic habitats across the North Atlantic from 3°C - 30°C (Block et al. 2001) and have the largest geographical distribution of pelagic fish in temperate waters (Bard et al. 1998, Fromentin and Fonteneau 2001). In general, bluefin migrate between warm spawning grounds and temperate feeding grounds (Fromentin and Powers 2005). Although bluefin spend the majority of time in the upper 50m of the water column, they also exhibit deep diving habits of up to 1000m (Block et al. 2001, Fromentin and Powers 2005).

### *Spawning Habitat*

Sea Surface Temperature (SST) is recognized as being of crucial importance for identifying the spawning habitat of Atlantic bluefin tuna. In the Gulf of Mexico, spawning occurs between 22.6-27.5 °C and between 22.5-25.5 °C in the Mediterranean (compilation of studies in Rooker et al. 2007). The spawning threshold is approximately 24°C in both the eastern and the western regions. This temperature threshold not only accounts for the differences in seasonal timing (e.g., starting in April in Gulf of Mexico April vs. May in Mediterranean), but also explains the finer scale distribution of spawning within each basin (Baglin 1982, Karakulak et al. 2004, Rooker et al. 2007). Evidence for Slope Sea spawning (Lutcavage et al. 1999, Richardson et al. 2016a,b, Hernandez et al. 2022) include the presence of larval bluefin at sampling stations with temperatures above 22°C (Hernández et al. 2022). Larvae have been sampled in the Slope Sea in May (Hernández et al. 2022), although modeling of oceanographic conditions have found July and August (peak) to be better suited to survivability (Rypina et al. 2019).

In addition to temperature, other variables are used to describe oceanographic conditions in which bluefin are found, whether for spawning or feed, including various chlorophyll metrics (e.g., CHL-a, gradCHL, ocean color: OC), salinity, currents, and sea surface height (e.g., Teo et al. 2007, Druon 2010, Druon et al. 2011, Druon et al. 2016). The availability of remote sensing and satellite technology to measure numerous oceanographic conditions is an asset for the research and management of a species with spatiotemporal distribution as expansive as bluefin tuna.

Druon et al. 2016 used ecological niche modelling (ENM) to predict the feeding and spawning habitats of various sized BFT in the Mediterranean Sea, the North Atlantic, and Gulf of Mexico. They used daily SST and the monthly increase of SST ( $\Delta\text{SST}_{30\text{days}}$ ), as well as factors such as chlorophyll-a fronts (gradCHL, horizontal gradient) and 3-day mean chlorophyll-a as a proxies for food availability, Sea Surface Height anomaly (SSHa), and Sea Surface Current Velocity (SSCV) to define suitable conditions for spawning and feeding compared to available presence

data. Their modeling identified potential spawning areas near the Azores and off Morocco to Senegal where there were no substantiated observations of spawning, nor did it identify the Slope Sea as a potential spawning area. Likewise, the model did not explain the actual presence of adult BFT between Florida and the Bahamas in the springtime (Druon et al. 2016), whose presence likely indicates the necessary migration between spawning and feeding grounds through suboptimal habitat.

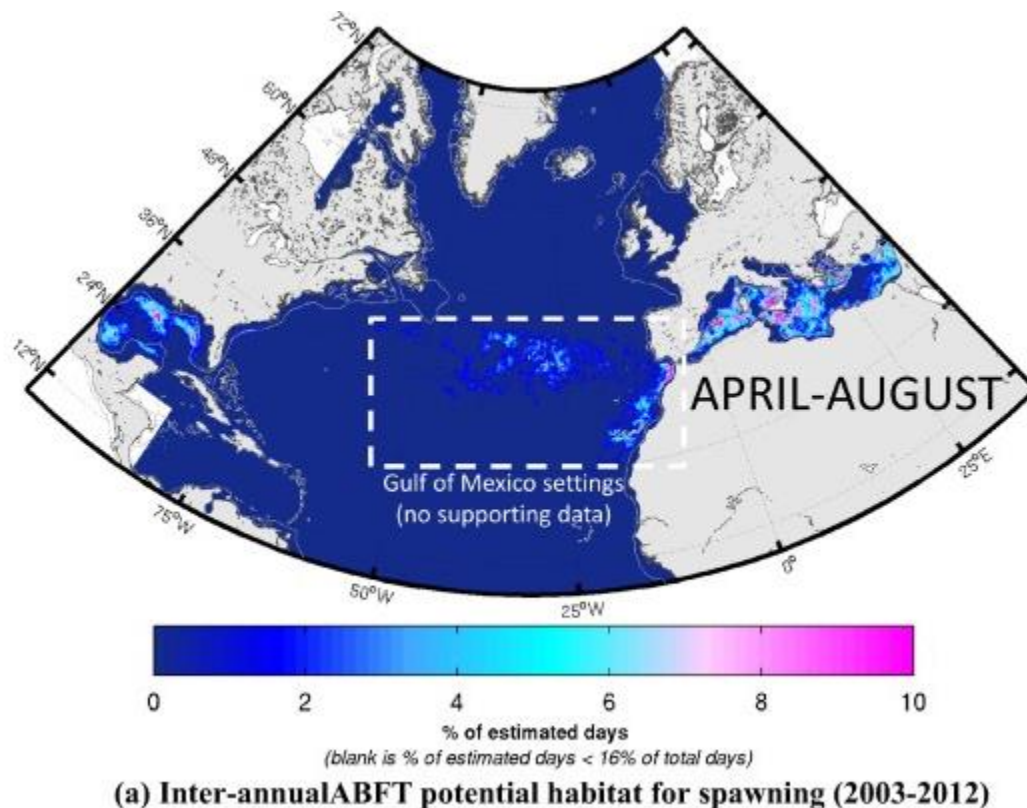


Figure 1. Druon et al. 2016 modelled suitable habitat for BFT spawning.

Hansell et al. 2020 investigated the correlation between the Atlantic Multidecadal Oscillation (AMO; index based on SST anomalies) and the Catch Per Unit Effort (CPUE) indices of the US rod and reel and Canadian surveys for western Atlantic bluefin tuna. The 2017 western bluefin stock assessment was the first to include a run with an environmental variable (AMO) to modulate catchability of two indices. Hansell et al. 2020 found that incorporating the AMO significantly improved model fit for the two indices, rectifying what had been a seemingly divergent pattern with the US index declining over time and the Canadian index increasing.

#### *Adult migrations and feeding ecology (i.e., movements, migrations, range shifts)*

Bluefin have been shown, via conventional, satellite, and natural tags, as well as genetics, to move great distances throughout their lives (Mather 1962, Wilson 1965, Fromentin and

Fonteneau 2001, Block et al. 2001, Galuardi and Lutcavage 2012, Siskey et al. 2016, Brophy et al. 2020, Kerr et al. 2020). In addition to natal homing (Rooker et al. 2008), another primary driver for bluefin migrations and movements is for feeding (Fromentin and Powers 2005).

Movements to feeding areas are dictated by the availability of prey. Distribution of prey is oftentimes dictated by water temperature and other oceanographic conditions (e.g., SST, CHL, gradCHL, SSHa) which indirectly controls the distribution of bluefin as an apex predator (Schick et al. 2004, 2009). Suitable oceanographic conditions for travel and prey (i.e., SST and SSS, and resultant thermoclines) have also been suggested as an explanation of the Brazilian Episode, when an ephemeral bluefin fishery thrived for during the 1960s in the Equatorial Atlantic (Fromentin et al. 2014). Factors such as temperature and salinity at depth (i.e., thermoclines) also influence prey aggregations and subsequently diving behavior of bluefin (Block et al. 2001). However, these factors may not be as readily measured from the ubiquitous SST data.

Research has shown bluefin to congregate in association with thermal fronts (Humston et al. 2000, Brill et al. 2002, Galuardi and Lutcavage 2012). Commercial fishermen often identify thermal fronts in SST and eddies as places to target for pelagic longlining, with bluefin tuna catch being highest around anticyclonic (warm core) eddies (Hsu et al. 2015).

Changes in prey distribution, whether influenced directly by water temperature or not, have been shown to alter foraging areas. As a direct result of warming waters, bluefin tuna have expanded their range to new areas east of Greenland, reaching as far as 65° N. This expansion is attributed to warming waters, influencing both the migration of BFT prey, Atlantic mackerel, and the subsequent movement of bluefin tuna to these areas (MacKenzie et al. 2014, Jansen et al. 2021). Feeding areas and efficiency have also been impacted by changes in prey distribution, including instances where the causes behind these changes remain unknown. One example is the interaction of eastward-moving Atlantic herring in the Gulf of Maine, which has led to alterations in the feeding areas and feeding efficiency of bluefin tuna (Golet et al. 2013, 2015). These range shifts can have important consequences for fisheries operating in traditional areas that can have repercussions on the perceived health of a given tuna stock (Golet et al. 2013).

### **Ecosystem Influences on Recruitment**

As noted, SST has a great influence on recruitment of bluefin tuna, as well as other oceanographic conditions. Larval bluefin habitat has been extensively studied and modeled, with several factors identified as important in the Gulf of Mexico, including SST, thermocline depth, and surface dynamics associated with the Loop Current (Muhling et al. 2010, Lindo-Atichati et al. 2012, Domingues et al. 2016, Alvarez et al. 2021), as well as food availability metrics such as zooplankton biomass and larval feeding behavior (Malca et al. 2022). Muhling et al. 2011 have noted that bluefin spawning typically occurs in areas with low chlorophyll-a (CHLa). Domingues et al. (2016) assessed spatiotemporal variability in the Gulf of Mexico from 1993 to 2011, leading to the development of the Bluefin\_Index. Their results suggested the

significance of Loop Current dynamics in the Bluefin\_Index. This work appears to be an improvement upon the previous spatial modeling work by Muhling et al. (2010), which explored a wide range of environmental factors (Figure 3):

**Table 2.** Pearson product moment correlations between all continuous environmental variables.

T100	<b>0.16</b>													
T200	<b>0.14</b>	<u><b>0.91</b></u>												
S0	-0.01	-0.03	-0.03											
S100	0.02	-0.04	-0.08	<b>0.12</b>										
S200	<b>0.08</b>	<b>0.73</b>	<u><b>0.78</b></u>	0.03	<b>0.23</b>									
Plankton log	-0.11	-0.03	-0.05	-0.03	0.04	-0.01								
Depth log	<b>0.31</b>	0.03	0.02	<b>0.14</b>	0.03	-0.01	-0.09							
Date	<b>0.62</b>	0.04	0.02	-0.13	-0.04	-0.05	-0.05	-0.01						
Time	0.05	0.03	0.02	0.001	-0.03	0.02	-0.07	-0.01	-0.04					
Wind	-0.26	-0.04	-0.02	0.03	-0.03	0.01	-0.05	-0.04	-0.22	0.004				
Moon phase	0.02	0.05	0.01	-0.01	-0.03	-0.03	-0.04	0.03	-0.05	0.003	0.04			
Longitude	<b>0.2</b>	0.05	0.03	<b>0.18</b>	<b>0.08</b>	0.05	<b>0.12</b>	<b>0.1</b>	-0.09	0.01	-0.17	0.05		
Latitude	-0.37	-0.1	-0.09	-0.13	-0.08	-0.1	<b>0.13</b>	-0.52	0.02	-0.02	<b>0.07</b>	-0.08	-0.11	
	T0	T100	T200	S0	S100	S200	Plankton log	Depth log	Date	Time	Wind	Moon phase	Longitude	Latitude

Temperature is abbreviated to 'T', and salinity to 'S', at the surface (0), 100 and 200 m depth. Significant correlations at  $P < 0.05$  are shown in bold, and strong correlations of  $r > 0.75$  are underlined.

They found that the index successfully captured the spatiotemporal variability and that this variability was linked to mesoscale ocean features such as currents (including cyclonic and anticyclonic patterns measured with SSH) and SST. Moreover, in comparison with age-0 recruitment, they found that 58% of recruitment variability was likely due to environmental conditions, and that the Loop Current may function as a trap for larvae, possibly lowering survival rates.

Modeling studies in the Mediterranean have included SST-related variables (Alvarez-Berastegui et al. 2016, Ingram et al. 2017, Reglero et al. 2019), Kinetic energy-related variables (Alvarez-Berastegui et al. 2016), CHLa-related variables (Alvarez-Berastegui et al. 2016), and other physical oceanographic features such as salinity and geostrophic current (Ingram et al. 2017). Temperature is important to larval bluefin as warmer temperatures are beneficial for egg and yoke-sac stages but are detrimental to feeding larvae that require more food under such conditions. Shropshire et al. (2020) described the Gulf of Mexico is oligotrophic, so mesoplankton variability and dynamics are critically important for larval pelagics that spawn there. As such, Fiksen and Reglero (2022) have found that bluefin time their spawning to benefit the feeding of larvae and climate change may shift phenology.

Likewise, Slope Sea habitats have also been studied and modeled by Hernández et al. (2022) who found that stations “most likely to contain bluefin larvae were identified as those with bottom depth exceeding 1000 m, sea-surface temperature (SST) exceeding 22 °C, and sea surface salinity of 34.5–36 PSU.” Additionally, Slope Sea larvae were found to be larger at age than Gulf of Mexico larvae.

The conventionally considered spawning and larval habitats of the Mediterranean Sea and Gulf of Mexico are significantly different from each other, with the Gulf of Mexico being warmer and with a more productive planktonic community. Despite this, Mediterranean larvae have been shown to have higher  $\delta N_{15}$  values than Gulf of Mexico larvae, indicating an elevated trophic position above the microzooplankton baseline, which may have important implications for future growth (Laiz-Carrión et al. 2015). However, García et al. (2017) attribute the higher  $\delta N_{15}$  values to maternal isotopic signatures as  $\delta N_{15}$  values were shown to decrease post-flexion. The preferred prey of Gulf of Mexico larvae is cladocerans and Malca et al. (2022) found that that growth rates correlated with prey availability. The variable distribution of preferred zooplankton prey in a diverse environment can potentially constrain growth (McGruck 1986, Shiroza et al. 2022). In warm oligotrophic systems such as the Gulf of Mexico, the high metabolic demands of bluefin tuna can make them susceptible to starvation when food availability is limited (Shopshire et al. 2021).

García et al. (2013) looked at daily growth variability of larval bluefin in the Balearic Sea (Western Mediterranean) and compared to temperature at a depth of 10 m, microzooplankton dry weight (MDW), and protein/dry weight ratio on larval growth: somatic and otolith growth rates were significantly related to temperature and MDW.

In Pacific bluefin tuna, reduction in temperature resulted in poor growth of juveniles (and assumed resulting in higher mortality), even if larval survival did not change. With models of larval drift, it is important to consider what SST larval would encounter and resulting growth and mortality (Kimura et al. 2010).

### **Ecosystem Influences on Growth and Maturity**

With an enormous range and distribution, the Atlantic bluefin tuna eat a wide variety of mesozooplankton, larger invertebrates, and fish throughout their lives, including everything from Cladocerans and *Illex* spp. squid, to sand lance (*Ammodytes* spp.) and round sardinella (*Sardinella aurita*), to Atlantic mackerel (*Scomber scombrus*) and Atlantic herring (*Clupea harengus*), to larger pelagic predators like Bluefish (*Pomatomus saltatrix*), and many things in between, they will eat almost anything that they can catch and fit into their mouths (Fromentin and Powers 2005, Golet et al. 2013, Nadeau 2021). Western bluefin tuna exhibit rapid growth in length and girth until about 185 cm (Mather and Schuck 1960), coincidentally the US commercial minimum size.

Eastern and Western bluefin grow and reach maturity at different rates, with Western fish growing faster after maturity and attaining larger sizes than their Eastern counterparts (ICCAT 1997). Eastern Atlantic bluefin tuna females, median size of maturity ( $L_{50}$ ) is 103.6 cm FL and age 3, and  $L_{100}$  is 135 cm FL and 4-5 years old (Corriero et al. 2005), and are considered mature at 15 kg (Rodríguez-Roda 1967). Western bluefin are known to take longer to reach maturity and at a larger size:  $L_{50}$  = age 6, and  $L_{100}$  = age 8, 200 cm, and 135 kg (Baglin et al. 1982, National

Research Council 1994). However, novel approaches for studying sexual maturity (ratios of hormones) have suggested that Western bluefin sexually mature closer to size/age of Mediterranean fish (Heinisch et al. 2014). Growth curves for both the Eastern and Western stocks are continuously being refined and updated (e.g., Rodríguez-Roda 1967, Corriero et al. 2005, Restrepo et al. 2010, Ailloud et al. 2017); however

Bioavailability of lipid stores may have profound effects on life history of bluefin, including somatic growth and gonadal development (Golet et al. 2015). Changes in prey distribution (see above) and condition has effects on tuna. Logan et al. (2015) used BFT stomachs, carbon and nitrogen stable isotopes, and lipid analysis from liver and white muscle samples to determine diet changes from late 1980s to early 2000s in the Gulf of Maine. They found that diet was similar across the time period, and overall lipid stores increase spring through fall, but lean fish were present in all seasons. Size of bluefin determined trophic position, mean TP = 3.9 for small tuna and TP = 4.9 for large tuna due to difference in diet preferences (sandlance *Ammodytes* spp. and euphausiids versus Atlantic herring *Clupea harengus*). Isotopic results were consistent with shelf vs. offshore baseline differences and variable seasonal distribution of bluefin in the Gulf of Maine that spend part of the year in the region for feeding.

Golet et al. (2015) investigated the linkage of prey (Atlantic herring) condition factor on bluefin condition in the Gulf of Maine, using energetics. Despite high prey abundance, tuna were doing poorly. Bluefin were found to be sensitive to changes in the size spectrum of prey rather than abundance; knock-on effects on were discovered in terms of distribution, reproduction, and economic value.

More directly linked to climate forces, Gordoa et al. (2021) looked at growth rates of young-of-year bluefin in the Mediterranean Sea and found significant differences in growth rates from different areas, with faster growth in the far east. They hypothesized that hatch date and associated water temperature influenced growth rates, suggesting that Atlantic BFT YOY is faster in the eastern Mediterranean, potentially due to the warmer conditions in that region, and that ontogenetic differences cannot be excluded as potential contributing factors. Gordoa et al. (2021) also hypothesized that climate induced changes, driven by water temperatures, altered the small pelagic ecosystem. These changes included an increase in round sardinella (*Sardinella aurita*) and higher species diversity, which could further impact the growth rates of Eastern bluefin tuna.

### **Ecosystem Influences on Natural Mortality**

For Atlantic bluefin tuna, natural mortality rate ( $M$ ) is not well characterized but assumed to be low due to long-lived nature of bluefin (Fromentin and Powers 2001). It appears that the proportion of males is higher in catch samples of large individuals, which might indicate a higher  $M$  or lower growth for female BFT (ICCAT 1997). Tagging from Southern bluefin tuna (*Thunnus maccoyii*) tends to confirm that  $M$  is higher for juveniles (between 0.49 and 0.24) compared to that of adults ( $\sim 0.1$ ) (Fromentin and Powers 2005, Block et al. 2019).



It is assumed that the main source of natural mortality in Atlantic BFT are large pelagic sharks and killer whales. Historical observations from the Dukedom of Medina Sidonia (southern Spain) and more recently indicate the occurrence of killer whales at the entrance of the Gibraltar Straits during the tuna spawning migration as well as at least bluefin caught in a “tonnara fissa”, a tuna trap, in 1972 in Sicily (Nortarbartolo di Sciara 1987). Guinet et al. (2007) hypothesize that orcas are likely more successful predators of juvenile bluefin using endurance-exhaustion hunting techniques but must rely on cooperative hunting methods for adults.

Various forms of flotsam (e.g., logs, barrels, buoys, etc.) have long been known to attract pelagic fishes and fisheries. However, the modern advent of Fish Aggregating Devices (FADs) (i.e., purpose-built/deployed devices) have been hypothesized to create conditions which actually increase natural mortality (i.e., separate from fishing mortality) by artificially aggregating smaller sized tunas that in turn are more susceptible to predation, as well as the potential to act as ecological traps that draw pelagic fish away from natural migration routes (Marsac et al. 2000). Although FADs are typically employed for tropical tuna fisheries (i.e., yellowfin *Thunnus albacares*, skipjack *Katsuwonus pelamis*, and bigeye *Thunnus obsesus*; Marsac et al. 2000), studies have shown that bluefin do aggregate to them (e.g., Sinopoli et al. 2004, Fayram and de Risi 2007), making the ecological trap phenomenon possible.

**Table**

Population Dynamic	Most frequent indicators from lit	Linkage to tuna	Primary Literature Sources	Data Sources	Relevance to management
Distribution and Habitat Use	Temperature (SST)	Spawning location and time	Karakulak et al. 2004, Rooker et al. 2007, Druon et al. 2016, Fiksen and Reglero 2022, Hernández et al. 2022, Druon et al. 2016, Galuardi and Lutcavage 2012, Hsu et al. 2015	MyOcean Consortium ( <a href="https://marine.copernicus.eu">https://marine.copernicus.eu</a> ) and Mediterranean Sea hydrodynamic model (NEMO-OPA v3.2)	Could inform management if new sub populations (e.g., Slope Sea) are identified)
		Prey distribution/availability			Changing prey distribution can draw bluefin to new areas
	Temperature (ΔSST30days)	Spawning location	Druon et al. 2016		
	AMO	Distribution of adults, e.g. US and Canadian catch indices	Hansel et al. 2020		Changing distribution of adults may influence assumptions of stock abundance
	Chlorophyll-a	Proxy for prey	Druon et al. 2016	MODIS-Aqua ocean color sensor, <a href="http://modis.gsfc.nasa.gov/">http://modis.gsfc.nasa.gov/</a>	



	SSHa/SSCV	Warm and cool core rings: proxy for temperature and prey	Druon et al. 2016	
	Salinity (SSS)	Spawning location	Hernández et al. 2022 Fromentin et al. 2014	
		Migratory routes		
<b>Recruitment</b>	Temperature SST	Spawning location	Alvarez-Berastegui et al. 2016	Could inform management if new sub populations (e.g., Slope Sea) are identified Impacts assumptions of stock assessment/MSE
		Larval mortality	Rypina et al. 2019	
	Chlorophyll-a (CHL, gradCHL)	Proxy for prey availability to larvae	Alvarez-Berastegui et al. 2016	
	Zooplankton biomass, feeding behavior	Prey availability for larvae	Malca et al. 2022	
	Ocean circulation	Water temperature and advection, how long larvae are in optimum areas	Rypina et al. 2019	
<b>Growth and Maturity</b>	Temperature (SST, T10)	Growth	Gordoa et al. 2021	Impacts assumptions of stock assessment/MSE
	Prey availability		Gordoa et al. 2021	
<b>Natural Mortality</b>	Orcas, sharks	Direct predation	Fromentin and Powers 2005	Impacts assumptions of stock assessment/MSE
	FADs	Ecological traps, draw away from natural migration routes, increased predation	Marsac et al. 2000	

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