Progress in Oceanography 142 (2016) 30–46

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Habitat suitability of the Atlantic bluefin tuna by size class: An ecological niche approach

Jean-Noël Druon [a,*], Jean-Marc Fromentin [b], Alex R. Hanke [c], Haritz Arrizabalaga [d], Dimitrios Damalas [a], Vjekoslav Tičina [e], Gemma Quílez-Badia [f], Karina Ramirez [g], Igor Arregui [d], George Tserpes [h], Patricia Reglero [i], Michele Deflorio [j], Isik Oray [k], F. Saadet Karakulak [k], Persefoni Megalofonou [l], Tevfik Ceyhan [m], Leon Grubišić [e], Brian R. MacKenzie [n], John Lamkin [o], Pedro Afonso [p], Piero Addis [q]

[a] European Commission, Joint Research Centre (JRC), Institute for the Protection and Security of the Citizen (IPSC), Maritime Affairs Unit, Via Enrico Fermi 2749, 21027 Ispra, VA, Italy
[b] IFREMER, Station de Sète, Avenue Jean Monnet, CS 30171, 34203 Sète Cedex, France
[c] Fisheries and Oceans Canada, St. Andrews Biological Station, 531 Brandy Cove Road, St. Andrews, NB E5B 2L9, Canada
[d] AZTI-Tecnalia, Marine Research Division, Herrera Kaia Portualdea z/g, 20110 Pasaia, Basque Country, Spain
[e] Institute of Oceanography and Fisheries, Šetalište Ivana, Meštrovića 63, 21000 Split, Croatia
[f] WWF Mediterranean Programme Office, C/ Canuda 37 3[er], 08002 Barcelona, Spain
[g] Dirección General de Investigación Pesquera en el Atlántico, Instituto Nacional de Pesca, Mexico
[h] Hellenic Center for Marine Research, Institute of Marine Biological Resources and Inland Waters, PO Box 2214, 71003 Heraklion, Greece
[i] Instituto Español de Oceanografía, Moll de Ponent, s/n, 07015 Palma de Mallorca, Balearic Islands, Spain
[j] Dipartimento di Scienze del Suolo, della Pianta e degli Alimenti (DISSPA), Università degli Studi di Bari Aldo Moro, Campus Universitario, Via Amendola 165/A, 70126 Bari, Italy
[k] Istanbul University, Faculty of Fisheries, Ordu st. No. 200, 34470 Laleli, Istanbul, Turkey
[l] Faculty of Biology, Department of Zoology-Marine Biology, University of Athens, Panepistimiopolis, Ilissia, 15784 Athens, Greece
[m] Ege University, Faculty of Fisheries, 35100 Bornova, Izmir, Turkey
[n] National Institute for Aquatic Resources (DTU Aqua), Technical University of Denmark, Charlottenlund Castle, DK 2920 Charlottenlund, Denmark
[o] NOAA/NMFS/SEFSC, 75 Virginia Beach Drive, Miami, FL 33149, USA
[p] Universidade dos Açores, Departamento de Oceanografia e Pescas, Rua Prof. Dr. Frederico Machado, 9901-862 Horta, Portugal
[q] Dipartimento di Scienze della Vita e dell'Ambiente, Università di Cagliari, Via Fiorelli 1, 09126 Cagliari, Italy

ARTICLE INFO

Article history:
Received 30 June 2015
Received in revised form 7 January 2016
Accepted 11 January 2016
Available online 14 January 2016

ABSTRACT

An ecological niche modelling (ENM) approach was used to predict the potential feeding and spawning habitats of small (5–25 kg, only feeding) and large (>25 kg) Atlantic bluefin tuna (ABFT), *Thunnus thynnus*, in the Mediterranean Sea, the North Atlantic and the Gulf of Mexico. The ENM was built bridging knowledge on ecological traits of ABFT (e.g. temperature tolerance, mobility, feeding and spawning strategy) with patterns of selected environmental variables (chlorophyll-a fronts and concentration, sea surface current and temperature, sea surface height anomaly) that were identified using an extensive set of precisely geo-located presence data. The results highlight a wider temperature tolerance for larger fish allowing them to feed in the northern – high chlorophyll levels – latitudes up to the Norwegian Sea in the eastern Atlantic and to the Gulf of Saint Lawrence in the western basin. Permanent suitable feeding habitat for small ABFT was predicted to be mostly located in temperate latitudes in the North Atlantic and in the Mediterranean Sea, as well as in subtropical waters off north-west Africa, while summer potential habitat in the Gulf of Mexico was found to be unsuitable for both small and large ABFTs. Potential spawning grounds were found to occur in the Gulf of Mexico from March–April in the south-east to April–May in the north, while favourable conditions evolve in the Mediterranean Sea from mid-May in the eastern to mid-July in the western basin. Other secondary potential spawning grounds not supported by observations were predicted in the Azores area and off Morocco to Senegal during July and August when extrapolating the model settings from the Gulf of Mexico into the North Atlantic. The presence of large ABFT off Florida and the Bahamas in spring was not explained by the model as is, however the environmental variables other than the sea surface height anomaly appeared to be favourable for spawning in part of this area. Defining key spatial and temporal habitats should further help in building spatially-explicit stock assessment models, thus improving the spatial management of bluefin tuna fisheries.

* Corresponding author. Tel.: +39 0332 78 6468.
E-mail address: jean-noel.druon@jrc.ec.europa.eu (J.-N. Druon).
URL: https://fishreg.jrc.ec.europa.eu/fish-habitat (J.-N. Druon).

http://dx.doi.org/10.1016/j.pocean.2016.01.002
0079-6611/© 2016 The Authors. Published by Elsevier Ltd.

1. Introduction

Atlantic bluefin tuna, *Thunnus thynnus* (Linnaeus, 1785), is a highly migratory species able to tolerate wide ranges of environmental conditions (Arrizabalaga et al., 2015) in tropical and temperate waters of the Atlantic Ocean and Mediterranean Sea. The earliest scientific reference on that species comes from Aristotle in his treatise History of Animals, written in 350 B.C., describing the migratory and reproductive habits of tuna in the Aegean and Black Sea (D'Arcy Wentworth Tompson, 1947). The two main ABFT populations are known to spawn in the Gulf of Mexico (western stock) and the Mediterranean Sea (eastern stock) respectively while the productive waters of the North Atlantic are the main feeding grounds. Adolescent fish are known to feed on the shelf of the North West Atlantic, in the North East Atlantic and in the Mediterranean Sea (e.g. Fromentin and Powers, 2005; Katavić et al., 2013; Rooker et al., 2008b). The habitat at the scale of the entire distribution of the species remains relatively unknown despite being heavily exploited recently. Total ABFT catches increased dramatically after the mid 80s, from less than 20,000 t up to more than 53,000 t in the mid 90s. Introduction of annual quota regulations by the International Commission of the Conservation of Atlantic Tunas (ICCAT) gradually reduced these numbers below 15,000 t in the mid 2000s (ICCAT, 2014). The recent overexploitation patterns of fish stocks led managers to more frequently require information on the distribution of marine resources, enabling them to identify the areas of most suitable habitat (European Commission, 2008; Rubec et al., 1999). Understanding the dynamics and spatial distribution of species is crucial for management, as spatial variability governs the definition of management units, stocks and boundaries (Fromentin and Powers, 2005). Herein we provide an approach for accomplishing such a task by delivering an indirect identification of the Atlantic bluefin tuna habitats based on the association between environmental traits and presence data. The relatively recent introduction of remote sensing and access to relevant data from the scientific community allowed for incorporating environmental data into distribution and abundance analyses. This has confirmed that bluefin tuna distribution is significantly affected by spatial and temporal variations of environmental conditions (see e.g. Fromentin et al., 2014). During their seasonal migrations, ABFTs seem to track changes in water temperature and currents, while they appear to preferably feed along frontal features (Druon et al., 2011; Royer et al., 2004; Schick et al., 2004). An attempt to associate presence data with several plausible factors affecting bluefin tuna distribution and abundance was recently undertaken by Druon et al. (2011) providing potential feeding and spawning habitats in the Mediterranean Sea.

In this paper, we link the ecological traits of small and large ABFTs to environmental variables (Ecological Niche Model approach, hereafter ENM) and investigate the respective feeding and spawning requirements. We used a large dataset of presence data and the literature for deriving the appropriate environmental envelope at the scale of the species distribution range (Gulf of Mexico, Mediterranean Sea and North Atlantic [defined as from 8.5°N to 74.0°N and from 82°W to 20°E outside of the other two areas]) and by size class (5–25 kg and above 25 kg, hereafter separating the small and large fish). The overlay of electronic tagging experiments and the potential habitats helped validate the model results and provide insights on the migration patterns important for understanding stocks dynamics. The seasonal and decadal habitat variability and spatial extent were discussed with respect to their potential impact on east and west ABFT stocks dynamics, as well as the utility on assessment and management.

2. Materials and methods

2.1. Description of the ecological niche modelling

The methodological approach used in our ENM is essentially composed of four main steps (Fig. 1), namely: (1) identify the main behaviours and ecological traits of ABFT based on literature; (2) collect and process the ABFT presence data and environmental covariates by geographical area; (3) derive a cluster analysis to identify a suite of relevant thresholds of environmental variables related to the ABFT ecology that describe the feeding and spawning habitat characteristics and finally (4) develop a habitat model to classify on a daily basis the degree to which each portion of the study area (model grid cell) is either suitable or unsuitable for each habitat (environmental envelope). All variables were projected on the finest horizontal grid of the satellite ocean colour data which was used (NASA MODIS-Aqua sensor), i.e. at the resolution of 1/24°.

2.2. Step 1 – specifying the ABFT habitats

This first step of ENM consists of identifying the relevant ecological traits of ABFT that link behaviours to its environment. We conducted a literature review and assembled an important and widely distributed dataset of ABFT presence data across the geographical areas (see Section 2.3). Royer et al. (2004) and Druon et al. (2011) already found that feeding ABFT is preferably located in the vicinity of chlorophyll-a frontal features so that the horizontal gradient of chlorophyll-a (hereafter gradCHL) is used as a proxy for food availability. A specific range of chlorophyll-a concentration (CHL) is also associated with that proxy. ABFT is one of the rare fish species to be thermo-regulated at about 20 °C (e.g. Carey et al., 1971; Carey and Lawson, 1973) and is able to occasionally dive to depths of >1000 m (Block et al., 2001) but spends most of its time in surface waters (79 ± 8% in the first 50 m from tagging studies, Walli et al., 2009). Large ABFTs have thus a rather large tolerance for temperature although it appears to be an important constraint for juvenile fish (Galuardi and Lutcavage, 2012). Therefore a specific range of sea surface temperatures (SST) was introduced to account for the thermal tolerance of both size classes while they feed. Sea surface height anomaly (hereafter SSHa) was tested as a variable potentially impacting the distribution of feeding habitat of both size classes. SSHa is mainly influenced by seasonal changes in temperature and currents that create eddies and gyres, i.e. divergent and convergent areas, potentially responsible for enhanced primary productivity and tuna prey aggregation (see examples in Hobday and Hartog (2014)). Arrizabalaga et al. (2015) and Teo and Block (2010) notably found that the temperate ABFT grows in colder and more productive environments with negative SSHa compared to tropical tuna species (with near null or positive SSHa).

ABFT spawning is known to occur in rather warm and mostly oligotrophic surface waters during spring. Parts of the Gulf of Mexico and Mediterranean Sea present such characteristics (Fromentin and Powers, 2005; Rooker et al., 2007). A specific CHL and SST range, as well as the monthly increase of SST (ΔSST_{30}), which simulates the spring stratification build-up, were selected to represent likely suitable spawning grounds (Druon et al., 2011). Additionally, a preferred range of SSHa was introduced for its potential role in food and larvae retention (see e.g. Bakun, 2013) as well as in transport from oligotrophic to mesotrophic areas. Intermediate levels of Eddy Kinetic Energy (EKE), which is derived from SSHa, were shown to strongly favour pelagic fish spawning (ABFT – Bakun, 2013; Teo et al., 2007; Teo and Block, 2010; Tuna species – Reglero et al., 2014; Small pelagic species – Asch and Checkley, 2013).