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Species composition of ichthyoplankton assemblages: a response to seasonal temperature changes

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Abstract

The 'mean temperature of the catch' (MTC; Cheung *et al.* 2013, *Nature* 497: 365-368.) was computed for 59 ichthyoplankton surveys conducted in several regions of the Eastern Mediterranean (off the coasts of Greece and Turkey) and in the Black and Marmara Seas. This covered 162 fish species whose preferred temperatures (PTs) were derived mainly from the data used to derive Aquamaps (see www.aquamaps.org). The (geometric mean) MTCs estimates from these 59 surveys correlated strongly with observed sea surface temperatures (SSTs), once account of the sampling regions was taken. Here, this relationship is quantified using a Type II or 'functional' (multiple) regression. Overall, the results suggested that the MTC could be an important descriptor of the taxonomic composition and temperature affinities of ichthyoplankton assemblages.

Keywords: Ichthyoplankton; mean temperature of the catch; Eastern Mediterranean Sea; Black Sea.

Introduction

While their body temperature can fluctuate with that of their environment, which can vary seasonally by over 10 °C or more, fish have preferred temperatures (PTs) for which their enzyme systems are optimized, and at which they perform best. This is also true for their eggs and larvae (ichthyoplankton) which, however, have narrower ranges of tolerated temperature (Pauly, 2010).

Because the PTs of fish are relatively stable, and can change only over evolutionary time, the taxonomic composition of fisheries catches can be used to infer a mean PT weighted by the catch of the component species, and thus to obtain a Mean Temperature of the Catch (MTC), shown, for example, to correlate, outside the tropics, with the increasing temperature of the habitats of fishes (Cheung *et al.,* 2013).

The principle at hand, i.e., the replacement in fisheries catches of fish with cold-water affinities, given increasing temperatures (in a given ecosystem) by fish from lower latitude regions (which cannot occur in the tropics, hence their exceptional situation), also applies to fish assemblages as obtained from surveys of juveniles and/or adults fish and invertebrates (Wichert & Lin, 1996; Collie *et al.,* 2008; Pinsky & Fogarty, 2012; Keskin & Pauly, 2014; Tsikliras *et al.,* 2015, 2018).

The MTC is tested here using a set of 59 ichthyoplankton surveys conducted in the Eastern Mediterranean, Marmara and Black Seas (Fig.1). We examine whether the taxonomic composition of ichthyoplankton assemblages, which largely reflects the timing of spawning in relation to the seasonal temperature cycle, can be summarized using MTCs. If species with cold-/warm-water affinities spawn in colder/warmer waters, the MTCs of ichthyoplankton surveys would be expected to correlate with ambient water temperatures.

Material and Methods

Table 1 provides key information on the ichthyoplankton surveys included here and the sea surface temperatures (SST) recorded during these surveys. Altogether, the surveys recorded 162 species of fish (Table S1, Supplementary Material), whose preferred temperatures (PTs) were estimated mainly from the temperature data used to draw the distribution range map in Aquamaps (see www.aquamaps.org). Each MTC estimate was assigned to a sampling date (the survey midpoint) and a location: Aegean Sea (AS), Black and Marmara Seas (BS), Levant Sea (LS) (Table 1).

The MTC for each survey was computed twice: (i) as the (arithmetic) mean of the PTs of the species in a survey, weighted by the number of their egg and/or larvae

Fig. 1: Location of the 59 ichthyoplankton surveys performed in the Eastern Mediterranean (Levant and Aegean Seas) in the Black and Marmara Seas from 1989 to 2014 and further documented in Table 1.

Table 1. Basic information on the ichthyoplankton surveys analysed here by season (Winter, Spring, Summer and Autumn), with the number of species (SPP), sea surface temperature (SST; ^{0}C) and mean temperature of the community (MTCa and MTCg, ^{0}C) computed as explained in the text.

#	Season	Sea	Haul type	SPP	SST	MTCa	MTCg	Reference
1	January 15, 1989	Aegean	horizontal	15	13.8	12.7	13.3	Hoşsucu and Ak (2002)
2	January 15, 1999	Black	vertical	2	10.2	9.5	9.4	Satılmış *et al.* (2003)
3	January 15, 2000	Levant	horizontal	11	17.0	17.9	18.4	Avşar and Mavruk (2011)
4	January 15, 2002	Black	vertical	2	10.2	9.6	9.8	Satılmış *et al.* (2006)
5	Dec. 21, 2006	Black	vertical	5	8.5	9.6	10.2	Klimova *et al.* (2009)
6	Dec. 15, 2008	Levant	horizontal	4	19.0	16.6	16.6	Mavruk (2009)
7	Feb. 15, 2015	Marmara	horizontal	5	9.8	9.9	10.8	Karademir (2015)
8	Feb. 15, 2015	Marmara	vertical	6	9.8	10.1	11.8	Karademir (2015)
Mean SPP, SST & MTC for all winter surveys				6	12.2	12.0	12.5	--
#	**Season**	**Sea**	**Haul type**	**SPP**	**SST**	**MTCa**	**MTCg**	**Reference**
9	May 15, 1999	Black	vertical	3	16.0	9.5	9.7	Satılmış *et al.* (2003)
10	May 15,1989	Aegean	horizontal	43	16.6	15.1	14.7	Hoşsucu and Ak (2002)
11	April 15, 1998	Aegean	oblique	23	22.6	12.0	14.3	Koutrakis *et al.* (2004)
12	May 15, 1999	Black	horizontal	13	16.0	11.5	12.7	Satılmış *et al.* (2003)
13	April 1, 1999	Levant	horizontal	5	18.6	17.9	17.9	Avşar and Mavruk (2011)
14	May 15, 2000	Levant	horizontal	5	18.6	21.2	19.8	Avşar and Mavruk (2011)
15	May 15, 2002	Black	vertical	4	16.0	11.1	11.8	Satılmış *et al.* (2006)
16	April 15, 2008	Levant	horizontal	25	20.9	17.0	17.6	Mavruk (2009)
17	May 15, 2015	Marmara	horizontal	14	17.6	12.4	14.4	Karademir (2015)
18	May 15, 2015	Marmara	vertical	10	17.6	14.4	15.1	Karademir (2015)
Mean SPP, SST & MTC for all spring surveys				14	18.0	14.2	14.8	--
19	July 15, 1988	Black	vertical	13	23.0	11.9	13.3	Klimova *et al.* (2014)
20	July 15, 1989	Aegean	horizontal	37	22.8	17.2	17.0	Hoşsucu and Ak (2002)
21	July 15, 1989	Black	vertical	10	23.0	14.8	13.7	Klimova *et al.* (2014)
22	July 15, 1990	Black	vertical	15	23.0	11.6	12.1	Klimova *et al.* (2014)
23	July 15, 1992	Black	vertical	5	23.0	11.6	12.4	Klimova *et al.* (2014)
24	June 11, 1993	Aegean	vertical	40	22.0	12.0	14.1	Somarakis *et al.* (2011)
25	June 22, 1994	Aegean	vertical	44	22.2	13.4	14.9	Somarakis *et al.* (2011)
26	June 22, 1995	Aegean	oblique	61	24.1	13.8	14.7	Somarakis *et al.* (2002)
27	June 19, 1995	Aegean	vertical	48	24.1	13.9	14.9	Somarakis *et al.* (2011)
28	June 13, 1996	Aegean	oblique	56	21.8	12.3	13.3	Somarakis *et al.* (2002)

continued

Table 1 continued

#	Season	Sea	Haul type	SPP	SST	MTCa	MTCg	Reference
29	June 10, 1996	Aegean	vertical	41	22.2	11.8	13.5	Somarakis *et al.* (2011)
30	July 1, 1997	Aegean	oblique	31	22.6	16.7	16.6	Koutrakis *et al.* (2004)
31	July 15, 1999	Black	horizontal	15	26.6	12.3	15.5	Satılmış *et al.* (2003)
32	July 15, 1999	Black	vertical	6	26.6	11.4	12.6	Satılmış *et al.* (2003)
33	July 15, 1999	Levant	horizontal	10	27.6	22.3	20.7	Avşar and Mavruk (2011)
34	July 15, 2000	Black	horizontal	24	21.7	12.4	14.6	Gordina *et al.* (2005)
35	July 15, 2000	Black	vertical	7	25.0	11.0	12.1	Gordina *et al.* (2005)
36	July 15, 2000	Black	vertical	13	21.7	12.8	14.4	Gordina *et al.* (2005)
37	July 15, 2001	Black	horizontal	28	24.3	12.7	14.6	Gordina *et al.* (2005)
38	July 15, 2001	Black	vertical	4	25.5	11.3	12.2	Gordina *et al.* (2005)
39	August 15, 2001	Black	vertical	33	26.1	12.2	15.7	İnce (2013)
40	July 2, 2002	Aegean	oblique	22	25.6	15.6	15.5	Tsikliras *et al.* (2009)
41	July 15, 2002	Black	vertical	7	26.6	13.8	14.1	Satılmış *et al.* (2006)
42	July 3, 2003	Aegean	oblique	25	24.9	14.6	14.8	Tsikliras *et al.* (2009)
43	June 6, 2003	Aegean	oblique	52	21.1	12.9	14.2	Isari *et al.* (2008)
44	June 6, 2004	Aegean	oblique	48	19.0	13.0	13.8	Isari *et al.* (2008)
45	June 8, 2005	Aegean	oblique	50	20.8	13.2	14.5	Isari *et al.* (2008)
46	June 24, 2006	Aegean	oblique	48	23.0	12.6	14.3	Isari *et al.* (2008)
47	July 15, 2007	Levant	horizontal	30	27.9	17.4	17.5	Mavruk (2009)
48	July 3, 2010	Black	vertical	21	23.0	12.1	14.4	Klimova *et al.* (2014)
49	August 15, 2014	Marmara	horizontal	13	24.9	11.3	13.4	Karademir (2015)
50	August 15, 2014	Marmara	vertical	9	24.9	11.3	14.0	Karademir (2015)
Mean SPP, SST & MTC for all summer surveys				27	23.7	13.3	14.5	--
51	Oct.15, 1989	Aegean	horizontal	42	21.6	16.9	15.1	Hoşsucu and Ak (2002)
52	Oct. 15, 1997	Aegean	oblique	33	22.5	15.3	16.3	Koutrakis *et al.* (2004)
53	Oct. 15, 1999	Levant	horizontal	11	24.0	19.0	18.3	Avşar and Mavruk (2011)
54	Oct. 15, 1999	Black	vertical	4	17.5	9.5	10.1	Satılmış *et al.* (2003)
55	Oct. 15, 2002	Black	vertical	3	17.5	13.4	12.6	Satılmış *et al.* (2006)
56	Oct. 10, 2005	Black	vertical	11	19.1	11.8	12.2	Klimova *et al.* (2010)
57	Oct.15, 2007	Levant	horizontal	18	25.7	14.3	17.1	Mavruk (2009)
58	Nov. 15, 2014	Marmara	horizontal	6	16.4	12.8	13.4	Karademir (2015)
59	Nov. 15, 2014	Marmara	vertical	2	16.4	10.3	10.2	Karademir (2015)
Mean SPP, SST & MTC for all autumn surveys				14	20.1	13.7	13.9	--

(MTCa) and (ii) as a (geometric) mean, to prevent the egg of larvae of a single or a few species from swamping the numbers for the community as a whole (MTCg). Here, the logarithm of the number of eggs and/or larvae each species contributed to an ichthyoplankton survey was multiplied by the PT of the corresponding species. The products were then added over all species and their sum divided by the sum of the species-specific logarithms of the eggs and/or larvae sampled.

Finally, we regressed the MTCs against SST. The three locations (Aegean Sea, Black and Marmara Seas and Levant Sea) were included in the regression models as 'dummy' variables (0 or 1) (Sokal and Rolf 1981). Given that this study did not intent to derive an equation for predicting MTC given SST (i.e., to obtain a 'predictive', or Type I regression; Ricker, 1973), but to characterize the relationship between these two key variables, a Type II or 'functional' regression was more appropriate. A Type I bivariate regression can be straightforwardly turned into a Type II regression by dividing its slope (b) by the correlation coefficient between the two variables (X and Y), and re-computing an intercept that satisfies = *a (b/r)**. This is equivalent to minimizing the squares of the deviations along both the abscissa and the ordinate (Ricker, 1973). With multiple regressions that include dummy variables, however, this procedure can be applied only to the continuous variables, as shown below.

Results

A single multiple regression which summarizes the data in Table 1, and explains 59 % of the variance is

$$MTCa = 8.441+0.161*SST+2.226*AS+5.468*LS \quad (1)$$

where MTCa is the arithmetic mean temperature of the ichthyoplankton assemblages (in ^{0}C), SST the surface temperature at the time of sampling (in ^{0}C), and AS and LS are the dummy variables referring to the sampling locations (see Table S1 in Supplementary Material).

The corresponding equation for MTCg (see Table S2 in Supplementary Material) explains 75 % of the variance and has the form:

$$MTCg = 9.000+0.188*SST+1.669*AS+5.027*LS \quad (2)$$

The fit is much better than for Equation 1, and hence our further considerations refer only to Equation 2.

The partial correlation (see Table S3 in Supplementary Material) between MTCg and SST, i.e., their correlation after the effects of the variables AS and LS were accounted for, was 0.507 (df=57, $p < 0.01$).

The slope linking MTCg and SST in Equation 2 is 0.188 (see above and Table S1 in Supplementary Material); hence, the Type II slope is $0.188/0.578 = 0.330$. Thus, we have:

$$MTCg = 5.604+0.330*SST+1.669*AS+5.027*LS \quad (3)$$

as our best summary of the data in Table 1 (see also Fig. 2).

Discussion

The mean temperature of the catch (MTC) concept was defined, set on a rigorous footing and shown to apply widely by Cheung *et al.* (2013), and subsequently confirmed by local studies, e.g., Tsikliras & Stergiou (2014) or Liang *et al.* (2018). Moreover, the 'C' in MTC can also be extended to communities, i.e., assemblages that are sampled at various places and whose taxonomic composition can be expected to yield MTC values that correlate with local temperatures, as shown, e.g., for the eastern Mediterranean by Tsikliras *et al.* (2015, 2018) and Keskin & Pauly (2018).

This is the first demonstration of a significant relationship between the MTC of ichthyoplankton assemblages and the SST at the time when and where these assemblages were sampled. A first insight from this is that geometric MTCs (i.e., MTCg) may be more appropriate than arithmetic MTCs for ichthyoplankton surveys, where a single species that happens to have spawned just before the survey is conducted can swamp an estimate (of MTCa) with an a huge number of eggs and larvae, and similarly for a very few species.

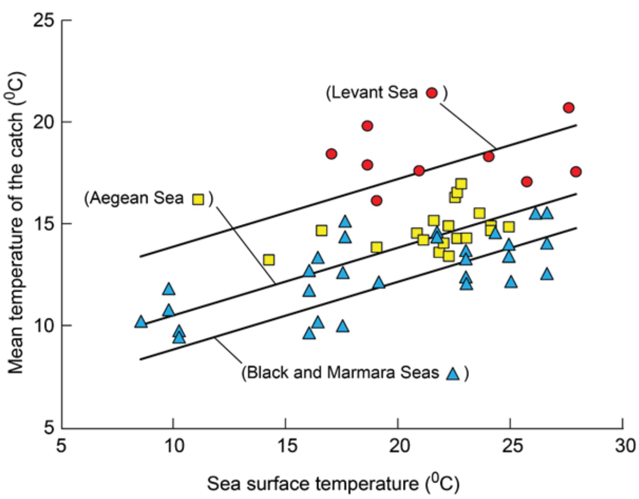

Fig. 2: Relationship between local SSTs and the (geometric) MTCs of 59 ichthyoplankton surveys in two regions of the Eastern Mediterranean (Levant and Aegean Seas) and in the Black and Marmara Seas, with the regression lines and the circles, squares and triangles pertaining to each region (see also Equation 2).

The dummy variables used to account for location generated patterns that were straightforward to interpret (Fig. 2). Thus, there was, in the SST/MTC space, a zone that none of the surveys occupied, i.e., low SST combined with high MTC. This implies that, in the Black Sea (where the coldest temperatures occur), the eggs and larvae of fish with cold water affinities dominate ichthyoplankton assemblages when SSTs are low. Conversely, in the Levant Sea, the MTCs are the highest in absolute term, and for any SST level, as befits an area with higher SST, and hence home to fish with warm-water affinities.

The only feature of Equations (2) and (3) that is not fully matching expectations is the value of the slope linking MTC and SST which, even when corrected as in Equation (3), is significantly lower than unity ($p < 0.05$).

Visual inspection of the data in Table 1 suggests that for some groups of surveys, MTC and SST have the expected 1:1 relationship (see also Figure 2). Thus, we suggest that a combination of noise due to taxonomic misidentifications, measurement errors and/or hidden parameters is the reason for this slope being < 1. Future studies may be devoted to reducing measurement errors: for example, by estimating PTs using a more rigorous method, and/or identifying additional predictors for MTC.

In the meantime, however, we are pleased to be able to report a surprising coherence among the results of 59 ichthyoplankton surveys and, in the process, to have established the usefulness of MTC as an indicator of the taxonomic composition and temperature affinities of ichthyoplankton assemblages.

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