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Ocean sunfish as indicators for the 'rise of slime'

David Grémillet[1,4,*], Craig R. White[2,4,*], Matthieu Authier[3], Ghislain Dorémus[3], Vincent Ridoux[3], and Emeline Pettex[3]

Overfishing and ocean warming are drastically altering the community composition and size structure of marine ecosystems, eliminating large bodied species [1]. Against a backdrop of such environmental change, the heaviest of all bony fish, the ocean sunfish (*Mola mola*), seems an improbable survivor. Indeed this indolent giant is killed globally as bycatch, and is listed as 'Vulnerable' [2]. We undertook the most extensive aerial surveys of sunfish ever conducted and found surprisingly high abundances off the Atlantic and Mediterranean coasts of Western Europe. With up to 475 individuals per 100 km^2, these figures are one order of magnitude higher than abundance estimates for other areas [3–5]. Using bioenergetic modelling, we estimate that each sunfish requires 71 kg day^{-1} of jellyfish, a biomass intake more than an order of magnitude greater than predicted for a similarly sized teleost. Scaled up to the population level, this equates to a remarkable 20,774 tonnes day^{-1} of predated jellyfish across our study area in summer. Sunfish abundance may be facilitated by overfishing and ocean warming, which together cause reduced predation of sunfish by sharks and elevated jellyfish biomass. Our combined survey and bioenergetic data provide the first-ever estimate of spatialized ocean sunfish daily food requirements, and stress the importance of this species as a global indicator for the 'rise of slime'. This hypothesis posits that, in an overfished world ocean exposed to global warming, gelatinous zooplankton should flourish, to the detriment of other mesotrophic species such as small pelagic fish, causing irreversible trophic cascades as well as a series of other environmental and economic issues.

Ocean sunfish are present around the globe in warm and temperate waters and are subjected to bycatch by long lines, drift gillnets and midwater trawls

in numerous fisheries [6]. The IUCN suspects that this species is declining globally by at least 10% per decade, and recommends further monitoring [2]. We flew a total of 98,520 km of aerial tracklines in the English Channel, the Atlantic and the Mediterranean, during one winter and one summer in 2011 and 2012, totalling 590 hours during which we observed 4,371 sunfish. Using our standardized observations in a distance-sampling analysis, we estimated an average density of 31 individuals per 100 km^2. Overall, for our 556,400 km^2 study region, we estimated total sunfish numbers to >54,000 and >290,000 individuals in winter and summer, respectively. Sunfish were generally more numerous in the Mediterranean than in the Atlantic (2,428 and 702 sightings, respectively), with a distribution hotspot in the SW Celtic Sea and in the Gulf of Lion, Western Mediterranean. In the latter area, there were up to 475 individuals per 100 km^2 in summer, with an average of 100 individuals per 100 km^2 during this season. Using bioenergetic modelling, we estimated that an average, 121 kg sunfish requires 71 kg of jellyfish per day to meet its energy requirements. Scaling up to our entire study area, this translates into 3,842 and 20,774 tonnes of jellyfish consumed each day by sunfish in winter and summer, respectively, with 12,869 tonnes daily consumption for the Mediterranean section in summer (Figure 1). In this region, an estimated minimum jellyfish abundance of 70 kg km^{-2} may therefore be required to feed the local sunfish population in summer.

These results, which are particularly novel with respect to the spatial ecology and energetics of sunfish, have far ranging implications for the biological oceanography of the oceans under the influence of global changes. Indeed, over the last decade there have been intense discussions around the 'rise-of-slime' concept [7]. Yet, there is limited large-scale, longitudinal information about the dynamics of jellyfish populations [8,9], even if recent work [10] conducted in the Irish Sea demonstrated that, over the 1994–2009 time period, jellyfish abundance correlated positively with sea-surface temperature over the preceding 18 months. Our sunfish observations off Western Europe and in the Mediterranean represent a snapshot and do not provide information about sunfish population trends over time, yet they
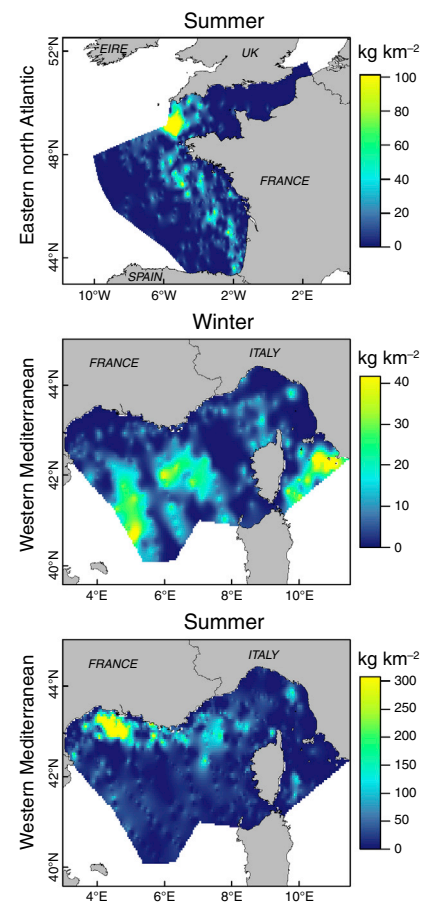

Figure 1. Estimated ocean sunfish predation on jellyfish.
Based on density of sunfish obtained from aerial surveys and estimates of rates of consumption from energetics modelling (colour scale, in total kg of jellyfish consumed by sunfish, per day and per km^2; colour scale range varies between graphs). Note sunfish mass occurrences in the Southwest Celtic Sea and the Gulf of Lion in summer. In winter, sunfish tend to be located farther offshore. Sunfish predation is not presented for the Eastern North Atlantic in winter because the limited number of observations (n = 22) precluded spatial modelling.

clearly show that these organisms are surprisingly abundant in areas that are notoriously overfished and exposed to ocean warming. Considering the massive consumption of gelatinous zooplankton by sunfish as indicated by our modelling work, high ocean sunfish numbers are suggestive of very substantial regional jellyfish stocks. As sunfish are far easier to monitor than gelatinous zooplankton, further investigations should aim at recording their spatio-temporal patterns of occurrence. Such longitudinal studies would provide a great opportunity to test

the rise-of-slime hypothesis, which is still highly controversial. Improved knowledge of ocean sunfish predatory pressure upon jellyfish will also lead to a better parametrization of ecosystem models in a changing ocean.

SUPPLEMENTAL INFORMATION

Supplemental Information including background, experimental procedures and two figures can be found with this article online at https://doi.org/10.1016/j.cub.2017.09.027.

REFERENCES

1. Payne, J.L., Bush, A.M., Heim, N.A., Knope, M.L., and McCauley, D.J. (2016). Ecological selectivity of the emerging mass extinction in the oceans. Science, https://doi.org/10.1126/science.aaf2416.
2. IUCN (2016). The IUCN Red List of Threatened Species.
3. Thys, T., and Williams, R. (2013). Ocean sunfish in Canadian Pacific waters: Summer hotspot for a jelly-eating giant? In 2013 OCEANS-San Diego (IEEE), pp. 1–5. Available at: http://ieeexplore.ieee.org/xpls/abs_all.jsp?arnumber=6740966 [Accessed January 3, 2017].
4. Houghton, J.D., Doyle, T.K., Davenport, J., and Hays, G.C. (2006). The ocean sunfish Mola mola: insights into distribution, abundance and behaviour in the Irish and Celtic Seas. J. Mar. Biol. Assoc. U.K. 86, 1237–1243.
5. Breen, P., Cañadas, A., Cadhla, O.Ó., Mackey, M., Scheidat, M., Geelhoed, S.C., Rogan, E., and Jessopp, M. (2017). New insights into ocean sunfish (Mola mola) abundance and seasonal distribution in the northeast Atlantic. Sci. Rep. 7, https://doi.org/10.1038/S41598-017-02103-6.
6. Pope, E.C., Hays, G.C., Thys, T.M., Doyle, T.K., Sims, D.W., Queiroz, N., Hobson, V.J., Kubicek, L., and Houghton, J.D.R. (2010). The biology and ecology of the ocean sunfish Mola mola: a review of current knowledge and future research perspectives. Rev. Fish Biol. Fish. 20, 471–487.
7. Jackson, J.B. (2008). Ecological extinction and evolution in the brave new ocean. Proc. Natl. Acad. Sci. 105, 11458–11465.
8. Pauly, D., Graham, W., Libralato, S., Morissette, L., and Palomares, M.D. (2009). Jellyfish in ecosystems, online databases, and ecosystem models. Hydrobiologia 616, 67–85.
9. Gibbons, M.J., and Richardson, A.J. (2013). Beyond the jellyfish joyride and global oscillations: advancing jellyfish research. J. Plankton Res. 35, 929–938.
10. Lynam, C.P., Lilley, M.K.S., Bastian, T., Doyle, T.K., Beggs, S.E., and Hays, G.C. (2011). Have jellyfish in the Irish Sea benefited from climate change and overfishing? Glob. Change Biol. 17, 767–782.

[1]Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry Montpellier - EPHE, Montpellier, France and FitzPatrick Institute, DST-NRF Centre of Excellence at the University of Cape Town, Rondebosch 7701, South Africa. [2]Centre for Geometric Biology, School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia. [3]Observatoire PELAGIS, UMS 3462 CNRS/Université de la Rochelle, 5 allées de l'océan, 17000 La Rochelle, France.
[4]Equal contribution.
*E-mail: David.gremillet@cefe.cnrs.fr (D.G.); craig.white@monash.edu (C.R.W.)

Correspondence

Non-cortical magnitude coding of space and time by pigeons

Benjamin J. De Corte[1,2],
Victor M. Navarro[3],
and Edward A. Wasserman[3,*]

Considerable research in cognitive science, neuroscience, and developmental science has revealed that the temporal, spatial, and numerical features of a stimulus can interact with one another [1,2], as when larger stimuli are perceived as lasting longer than smaller stimuli. These findings have inspired the prominent hypothesis that time, space, and number are processed by a 'common magnitude system', which represents these dimensions via the same unit of magnitude [3,4]. According to current theorizing, the parietal cortex mediates this system [4]. To test the species generality and neuroanatomical foundations of this hypothesis, we asked whether space–time interactions can be observed in birds. Unlike mammals, birds lack a cortex [5,6]; rather, they possess a neuron-dense pallium that is organized in clusters, in contrast to the laminar structure of the mammalian cortex [7]. Despite these striking neuroanatomical disparities, we observed reliable space–time interactions in pigeons. Our findings suggest that common magnitude systems are more widespread among animals than previously believed and need not be cortically dependent in all species.

To explore this common magnitude hypothesis, we assessed whether pigeons would show cross-dimensional interactions using a task devised by Merritt et al. [8], which produces space–time interactions in humans and nonhuman primates. Specifically, across intermixed training trials, we taught pigeons to judge the spatial-length or the temporal-duration of a horizontal line — spatial and temporal tasks, respectively. After presenting the line, pigeons were shown two choice stimuli. For

the spatial task, if the line-length was short (6 cm), pigeons received food for pecking one choice stimulus; but if the line-length was long (24 cm), pigeons received food for pecking the other choice stimulus. Similarly, for the temporal task, pigeons received food for pecking one of two different choice stimuli depending on whether the duration of the line had been short (2 s) or long (8 s).

During testing, we introduced intermediate values for the length of the line in the spatial task and for the duration of the line in the temporal task. Critically, we also varied the values of the *irrelevant* dimension to see if this would affect how pigeons judged the *relevant* dimension. Specifically, in the spatial task, we presented the line for either a shorter or longer duration than in training; similarly, in the temporal task, we presented shorter or longer line-lengths than in training.

Figure 1 depicts the proportion of '*long*' responses as a function of the magnitude of the relevant dimension during the spatial and temporal tasks. As expected, these values increased as the magnitude of the stimulus being judged increased. More importantly, varying the *irrelevant* dimension systematically affected judgments of the *relevant* dimension.

We first quantified this effect by calculating the Point of Subjective Equality (PSE) for each trial type. The PSE is the relevant dimension value that was equally likely to be reported as short or long. Increases or decreases in this measure indicate an increased tendency for stimuli to be judged as short or long, respectively. For the spatial task, presenting the line for a short, medium, or long period of time yielded PSEs of 21.37, 18.95, and 15.14 cm, respectively. Similarly, for the temporal task, varying the spatial-length of the line to be short, medium, or long produced PSEs of 6.60, 5.90, and 4.42 s, respectively.

Next, we analysed the data using a mixed-effects logistic regression model (Supplemental Information). In the spatial task, short and long line-durations caused the overall proportion of long-length choices to decrease and increase, respectively (Short-duration line: $B = -0.72$,