Marine Heat Waves in the Mediterranean Sea: A Semi-Quantitative Synthesis with a Focus on Biological Responses

Toplinski valovi u Sredozemnom moru: polukvantitativni pregled s naglaskom na biološke odgovore

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Abstract

Marine heatwaves are periods of anomalously high seawater temperatures lasting for a minimum of five days. They are recognised as one of major stressors in marine environments over the past decade with consequences for biodiversity, ecosystem functioning, and the use of marine resources. Although marine heatwaves have been reviewed at the global scale, Mediterranean-specific biological and ecological evidence remains scattered, making it difficult to identify consistent response patterns, research biases, and priorities for monitoring and management. Here, we provide a semi-quantitative synthesis of research on Mediterranean marine heatwaves, focusing on biological and ecological responses. The review followed PRISMA 2020 guidelines based on records retrieved from the Web of Science Core Collection. Of the 205 records initially identified, 142 peer-reviewed studies published between 2007 and 2025 met the inclusion criteria. Publication output increased strongly after 2021, with biology and ecology representing the dominant research focus. Across the complete dataset, modelling was the most frequently used approach. By contrast, biological and ecological studies relied mainly on laboratory experiments and field observations. The species-level analysis revealed a taxonomic bias over the phyla Tracheophyta, Mollusca and Cnidaria. Most studies examined multiple traits, particularly combinations of physiology and growth, whereas genetics, cellular responses, microbiome, behaviour, and biochemical composition were less studied. In addition, there is a lack of research on commercially important species. Overall, Mediterranean marine heatwave research is expanding rapidly, but the field is currently taxonomically narrow, methodologically fragmented and lacks focus on management and policy needs. By identifying these biases, this review provides a regional framework for directing future research towards long-term biological monitoring, broader taxonomic coverage, commercially relevant species and the integration of ecological evidence into adaptation strategies.

KEY WORDS

marine heat waves
research focus
research methods
biological and ecological traits

Sažetak

Toplinski valovi u moru jesu razdoblja iznadprosječno visokih temperatura mora koja traju najmanje pet uzastopnih dana. Tijekom posljednjeg desetljeća prepoznati su kao jedan od glavnih stresora u morskom okolišu s posljedicama na bioraznolikost, funkcioniranje ekosustava i korištenje morskih resursa. U ovom radu donosimo polukvantitativni pregled istraživanja toplinskih valova u Sredozemnom moru, s osvrtom na biološke i ekološke značajke. Pregled literature slijedio je PRISMA 2020 smjernice, na temelju zapisa preuzetih iz baze Web of Science Core Collection. Kriterije uključivanja u analizu zadovoljila su 142 članka od ukupno 205. Broj članaka značajno se povećao nakon 2021. Godine, pri čemu su biologija i ekologija bile dominantna područja istraživanja. U cjelokupnom skupu podataka modeliranje je bilo najčešće korišten pristup tijekom istraživanja. Nasuprot tome, biološka i ekološka istraživanja uglavnom su se oslanjala na laboratorijske pokuse i terenska opažanja. Analiza na razini vrsta pokazala je taksonomsku pristranost prema koljenima Cnidaria, Tracheophyta i Mollusca. Većina istraživanja proučavala je više značajki, a osobito su bile brojne kombinacije fiziologije i rasta, dok su genetika, stanični odgovori, mikrobiom, ponašanje i biokemijski sastav slabije istraženi. Osim toga, nedostaju istraživanja komercijalno važnih vrsta. Broj članaka usmjeren na toplinske valove u Sredozemnom moru raste, ali je područje istraživanja trenutačno taksonomski ograničeno, metodologija nije ujednačena te je nedovoljno usmjereno na potrebe upravljanja i politika. Rezultati ovog rada pružaju regionalni okvir za usmjeravanje budućih istraživanja prema dugoročnom biološkom praćenju stanja, širem taksonomskom obuhvatu, komercijalno važnim vrstama te uključivanju znanstvenih spoznaja u strategije prilagodbe.

KLJUČNE RIJEČI

toplinski valovi u moru
težište istraživanja
metode istraživanja
biološko-ekološke značajke

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1. INTRODUCTION / *Uvod*

Marine heatwaves (MHWs) are defined as discrete periods of anomalously high sea surface temperature lasting for at least five consecutive days, during which temperatures exceed the 90th percentile relative to a climatological baseline [1]. In the last two decades they have increased in frequency, longevity, intensity and spatial distribution [2, 3]. MHWs are not limited only to the surface layer of the seawater, instead they can occur at any depth, in any ocean basin and at any time of the year [4]. Negative impacts on marine ecosystems are already well documented worldwide, such as coral bleaching, mass mortality events or shifts in distributions of species [5].

The Mediterranean Sea is one of the world's regions most vulnerable to global stressors, including climate change and marine heatwaves. It has semi-enclosed configuration, high evaporation rates, and limited exchange with the Atlantic Ocean which all together contribute to the heat accumulation and stronger summer stratification. These conditions can extend thermal anomalies into subsurface layers and reduce the vertical uptake of nutrients to surface waters [6]. The Mediterranean basin warmed approximately 0.038–0.040°C per year from 1982 to 2020 which is more than three times the global ocean average [7, 8]. Additionally, the period 2015–2019 was the warmest recorded since the start of satellite observations in 1982, with mean temperatures 1.2°C above the 1982–1986 baseline. Since 2012, more than 75% of the Mediterranean surface has been affected by strong or higher-category MHWs [8]. Under high-emission trajectories, the mean sea surface temperature of the Mediterranean could reach 24.32°C by 2100, compared with the observed mean of 20.16°C for 1992–2021 (Rosselló et al., 2023). Projections are also severe under the most optimistic low-emission scenario: by 2050, 90% of climate models indicate more than 189 MHW days per year in the Mediterranean, when assessed against a fixed historical baseline [9]. If warming continues, the basin is expected to face progressively longer lasting and more severe events throughout the 21st century [10].

Although it accounts for only 0.32% of the total ocean volume, the Mediterranean Sea has exceptionally high marine biodiversity, with estimated 7-10% of all known marine species highlighting it's both ecological and socio-economic importance [11, 12]. Negative impacts of warming trend have already been reported. Mass mortality events were recorded in 1999 and 2003 along the northwestern Mediterranean coast. More than 40 species from several taxonomic groups were affected, including cnidarians, sponges, bivalves, and bryozoans [13, 14, 15]. Furthermore, widespread mortalities were documented across the basin during the 2015–2019 period. These events affected 50 taxa from eight phyla and occurred across all major coastal habitat types. In some species, mortality reached up to 80% of surveyed populations [8]. Recent research has shown marked sensitivity to thermal stress of the endemic seagrass *Posidonia oceanica* (Linnaeus) Delile, 1813, with documented declines in shoot density, growth, and reproductive output [16, 17]. All levels of biological organisation can be impacted by MHWs, from cellular and physiological disruption to changes in community structure [5, 18]. Moreover, MHWs can interact with other pressures such as ocean acidification, eutrophication, and fishing [5, 19]. Socio-economic effects are beginning to be reported as well, including temperature-driven mortality in commercially important species such as *Mytilus galloprovincialis* Lamarck, 1819 [20, 21].

While previous reviews have provided broad syntheses of marine heatwave impacts [2, 5, 6, 9], Mediterranean-specific biological and ecological evidence remains scattered across taxa, methods, and response traits. A regional synthesis is therefore needed to assess how well current research addresses the ecological and socio-economic priorities of the Mediterranean region and to identify potential methodological and taxonomic research gaps.

To address this, we conducted a semi-quantitative review of up-to-date Mediterranean MHW research. The specific aims were to: (1) identify trends in publication output, research focus, and study types; (2) quantify taxonomic representation and identify possible research biases; and (3) synthesise current knowledge on biological responses and define the main knowledge gaps.

2. MATERIALS AND METHODS / *Materijali i metode*

2.1. Literature search and study identification / *Pretraživanje literature i identifikacija radova*

A systematic literature review was carried out following the PRISMA 2020 guidelines to ensure transparency, reproducibility, and methodological rigour [22]. The full screening and selection procedures are presented in the PRISMA flow diagram (Figure 1).

The literature search was performed in the Web of Science Core Collection database (Clarivate Analytics) on January 15, 2026. The search string was applied to the Topic field (TS), which includes titles, abstracts, and keywords:

TS= (("marine heatwav*" OR "marine heat wav*" OR "ocean* heatwav*" OR (MHW* NEAR/3 (marine OR ocean* OR sea*))))

AND

TS= (Mediterran* OR "Mediterranean Sea" OR "Mediterranean Basin" OR "Med Sea" OR "Alboran Sea" OR "Balearic Sea" OR "Gulf of Lion" OR "Ligurian Sea" OR "Tyrrhenian Sea" OR "Adriatic Sea" OR "Ionian Sea" OR "Aegean Sea" OR "Levantine Sea").

Articles were selected using predefined inclusion and exclusion criteria (Table 1).

Table 1 Predefined inclusion and exclusion criteria applied during articles screening

Tablica 1. Kriteriji uključivanja i isključivanja primijenjeni pri odabiru radova

Criterion	Inclusion	Exclusion
Publication type	Peer-reviewed article or review	Editorial, commentary, dataset, preprint
MHW focus	Explicit	Absent or only indirect
Geographic scope	Mediterranean Sea	Outside Mediterranean
Study type	Empirical, experimental, observational, modelling	None of the above
Record status	Unique	Duplicate

The initial search returned 205 articles. Screening was carried out in two stages: (1) title and abstract screening, and (2) full-text eligibility assessment when title and abstract information was insufficient to determine eligibility. After screening, 142 studies were retained for full analysis. In total,

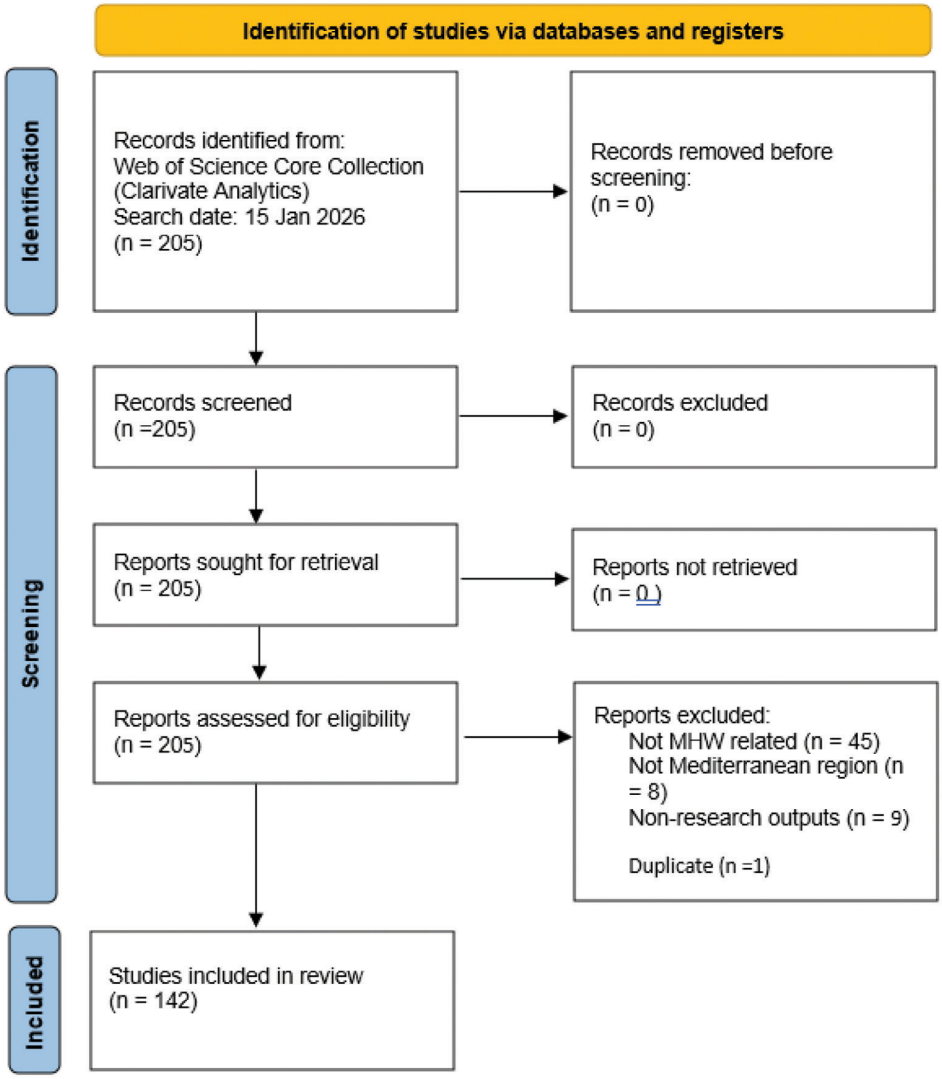


Figure 1 PRISMA 2020 flow diagram of literature search in Web of Science Core Collection on marine heat waves in the Mediterranean Sea

Slika 1. PRISMA 2020 dijagram tijeka pretraživanja literature u bazi Web of Science Core Collection o toplinskim valovima u Sredozemnom moru

Source: Authors

63 records were excluded. 45 studies were not directly relevant to MHWs, eight were conducted outside the Mediterranean region, 10 did not qualify as appropriate publication type (dataset, commentary, editorial) and one article was a duplicate record. Data from all included articles were entered into a standardised spreadsheet (Microsoft Excel). The following variables were recorded for all studies:

1. Bibliographic information: Title, Authors, Year of publication, Journal, DOI
2. Research focus: Biology/Ecology, Climatology/Oceanography, Combined, Management/Policy - classified based on the primary objective as stated in the abstract and introduction. For studies classified as Biology/Ecology, the following additional variables were extracted:
3. Methodological approach: Laboratory experiment, Field observation, In-situ experiment, Modelling, Monitoring, Combined, Other
4. Level of biological organisation studied: Species, Multiple species, Community, Other
5. Taxonomic information: Species latin name, Phylum, Life stage
6. Studied traits: Physiology, Growth, Reproduction and larval development, Behaviour, Genetics, Cellular processes, Biochemical composition, Combination
7. Relevance: Commercial, Ecological. Commercial relevance was assigned if the species is recognised as commercially exploited or cultured in the Mediterranean. Ecological relevance was assigned to all remaining species.

To assess taxonomic research effort, analyses were also conducted at the species-record level. Articles that included more than one species contributed a separate entry for each organism. This was considered the most appropriate unit of analysis for quantifying research effort across taxa, because the number of species studied reflects the biological scope of the literature independently of article count.

Data processing and visualisation were conducted in R version 4.6.0 [23] using the readxl, dplyr, tidyr, and ggplot2 packages. All analyses were descriptive. Frequencies were calculated as the number of records assigned to each category, and percentages were calculated relative to the relevant denominator: the full dataset of included studies, the biology/ecology subset, or the species-record dataset, as indicated in the text and tables.

3. RESULTS / *Rezultati*

3.1. Overview of publication output and research categories / *Pregled objavljenih radova i znanstvenih područja*

A total of 142 articles published between 2007 and 2025 met the inclusion criteria. Publication output was strongly concentrated in the most recent period, with most studies published from 2021 onward (Figure 2). Biology and ecology were the dominant research focus, followed by climatology and oceanography, whereas management/policy-oriented research was rare and appeared only from 2022 onward (Table 2).

Modelling was the most common methodological approach across the dataset. The majority of modelling studies originated from climatology and oceanography data with only 12 addressing biological or ecological questions.

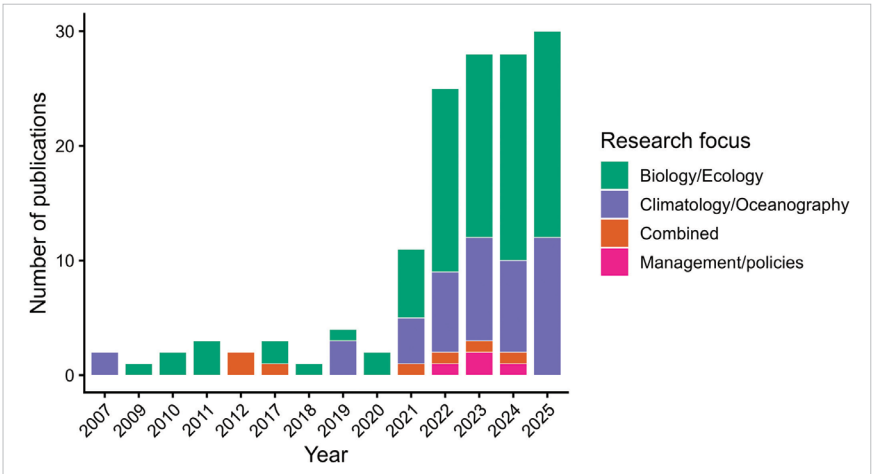


Figure 2 Number of included marine heatwave studies published per year from 2007 to 2025, colour-coded by research focus

Slika 2. Broj uključenih radova o toplinskim valovima objavljenih po godinama od 2007. do 2025., s prikazom boja prema istraživačkom fokusu

Source: Authors

Table 2 Summary articles included in systematic synthesis

Tablica 2. Sažetak članaka uključenih u sustavnu sintezu

A. General overview	n	%
Total included articles	142	100.0%
Year range	2007–2025	—
Studies published 2021–2025	122	85.9%
Studies published before 2021	20	14.1%
B. Research focus (n = 142)	**n**	**%**
Biology/Ecology	86	60.6%
Climatology/Oceanography	45	31.7%
Combined	7	4.9%
Management/policies	4	2.8%
C. Study type - all studies (n = 142)	**n**	**%**
Modelling	60	42.3%
Laboratory experiment	26	18.3%
Field observation	26	18.3%
In situ experiment	13	9.2%
Combined approaches	8	5.6%
Monitoring	7	4.9%
Other	2	1.4%
D. Study type - biology/ecology only (n = 86)	**n**	**%**
Laboratory experiment	26	30.2%
Field observation	25	29.1%
Modelling	12	14.0%
In situ experiment	11	12.8%
Combined approaches	7	8.1%
Monitoring	5	5.8%

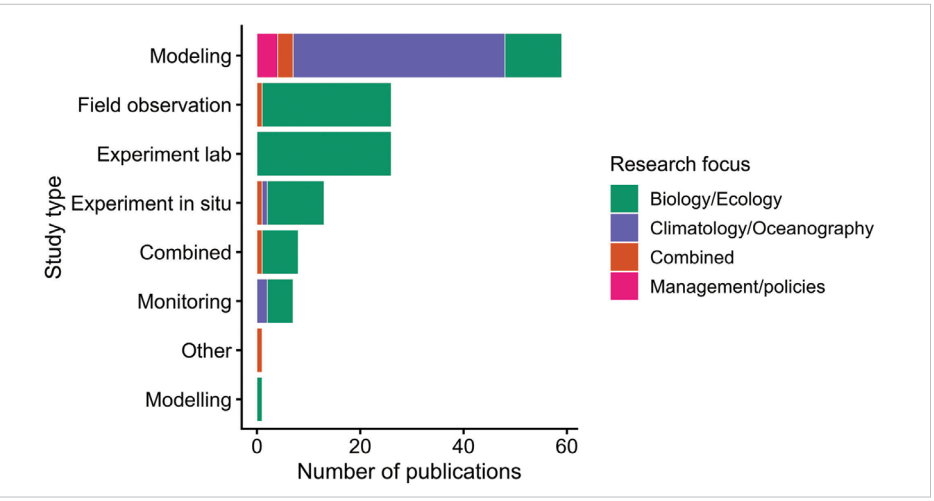


Figure 3 Distribution of study types among included marine heatwave studies, colour-coded by research focus

Slika 3. Raspodjela tipova radova među uključenim istraživanjima o toplinskim valovima u moru s bojama prema istraživačkom fokusu

Source: Authors

Field observations and laboratory experiments were equally represented, followed by in situ experiments, combined approaches and monitoring studies (Figure 3).

3.2. Biological and ecological research / *Biološka i ekološka istraživanja*

Further analyses were applied to the 86 studies classified under biology and ecology. Within this subset, laboratory experiments and field observations were the most frequently used approaches, accounting for nearly 60% of studies. Modelling accounted for 14% followed by in situ experiments, combined approaches, and monitoring (Table 2).

The species-level analysis included 98 records from 86 biological studies. Phylum Tracheophyta was the most studied, accounting 26.3%, followed by Mollusca (19.3%) and Cnidaria (15.8%). Together, these three phyla comprised 61.4% of all species-level biological records, indicating a focus of research effort on a limited number of taxa.

Trait data were extracted from all records. Studies assessing multiple traits simultaneously (hereafter "Combination") were the most frequent, accounting for 46.9%. Among single-trait categories, physiology (14.2%) and community structure (9.2%) were the most common, followed by growth (8.2%) and reproduction and larval development (7.1%). Microbiome (4.1%), behaviour (4.1%), and genetics (3.1%) were comparatively rare, while cellular responses (2%) and biochemical composition (1%) were the least represented categories (Figure 5). To further characterise the combination records, trait co-occurrences within the 46 combination studies were examined. The most common pairing was physiology combined with growth. followed by genetics combined with physiology, and community structure combined with either physiology or growth.

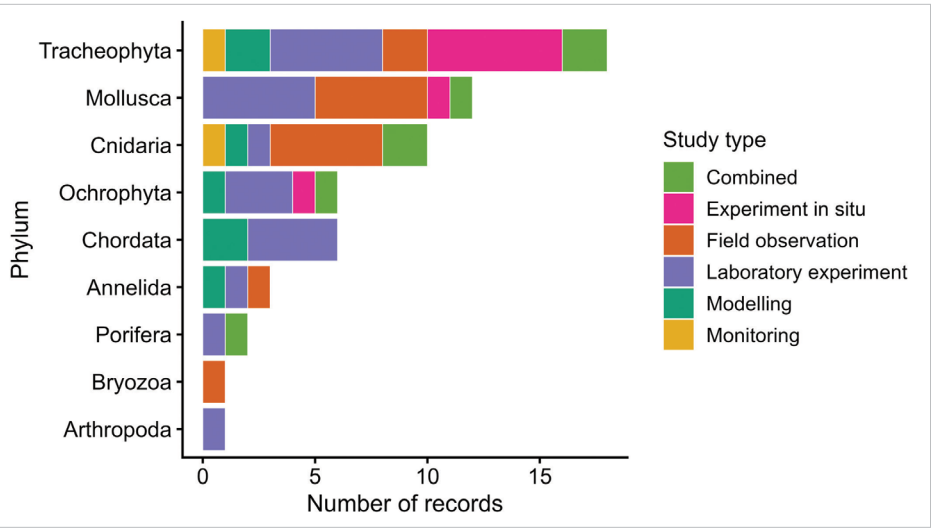


Figure 4 Distribution of single-taxon biological records across phyla in Mediterranean marine heatwave studies, colour-coded by study type. Each record represents an individual species-level observation extracted from the literature

Slika 4. Raspodjela bioloških zapisa pojedinačnih svojti po koljenima u mediteranskim studijama o toplinskim valovima, s bojama prema tipu studije. Svaki zapis predstavlja pojedinačno opažanje na razini vrste iz literature

Source: Authors

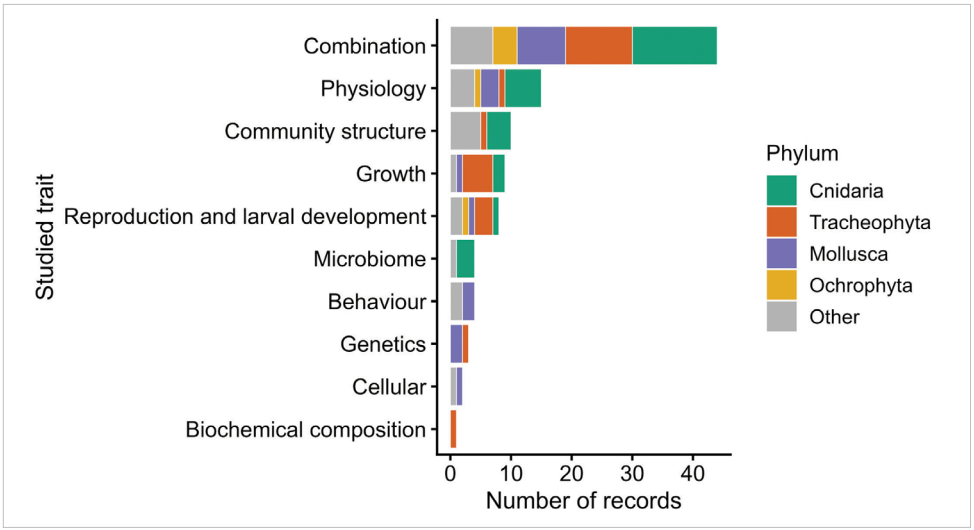


Figure 5 Distribution of studied biological traits in Mediterranean marine heatwave research, colour-coded by phylum. Only major phyla are shown separately, while less represented groups are combined into "Other". Each record represents a species-level observation

Slika 5. Raspodjela proučavanih bioloških svojstava u mediteranskim istraživanjima o toplinskim valovima, s bojama prema koljenu. Zasebno su prikazana samo glavna koljena, dok su manje zastupljene skupine objedinjene u „Ostale". Svaki zapis predstavlja opažanje na razini vrste

Source: Authors

Among the 98 species-level records, 20 were assigned commercial relevance. Molluscs represented the largest commercially relevant group (n = 14 records), with *M. galloprovincialis* being the most frequently studied species (n = 5), followed by *Chamelea gallina* (Linnaeus, 1758) (n = 2), and single records each for *Perna perna* (Linnaeus, 1758), *Magallana gigas* (Thunberg, 1793), *Venerupis corrugate* (Gmelin, 1791), *Ruditapes decussatus* (Linnaeus, 1758), *Ruditapes philippinarum* (A. Adams & Reeve, 1850) and *Cerastoderma edule* (Linnaeus, 1758). Fishes contributed to four commercial records: *Diplodus sargus* (Linnaeus, 1758) (n = 2), *Seriola dumerili* (Risso, 1810) (n = 1), and *Dicentrarchus labrax* (Linnaeus, 1758) (n = 1). Two additional commercially relevant species fell outside these groups: *Corallium rubrum* (Linnaeus, 1758) (Cnidaria; n = 1) - a protected species with significant commercial history in the Mediterranean, and *Procambarus clarkii* (Girard, 1852) (Crustacea; n = 1).

4. DISCUSSION / *Rasprava*

The significant increase in publications after 2021 indicates that research on marine heatwaves in the Mediterranean region has responded to the more frequent and more intense MHW events in the past couple of years [2, 5]. Those events also provided field conditions suitable for observational and monitoring studies across the basin [6, 9]. The dominance of studies focused on biology and ecology suggests that research effort has been directed towards the responses of marine species and ecosystems to MHWs. The small number of management- and policy-oriented studies probably reflects the usual delay between the accumulation of ecological evidence and its incorporation into governance frameworks [27]. Three studies published so far address topics such as aquaculture adaptation [24], prioritisation in seagrass management [25], and the role of marine protected areas [26]. Although this may still represent a limited response to recent events, it remains an important direction for defining future priorities.

There was a difference in methodological approaches between the whole dataset and the biology/ecology subset of papers. Across all studies, modelling was the most common methodological approach. That fact is probably linked to the availability of long-term physical datasets and satellite observations (e.g. Copernicus marine service). Biological and ecological studies were mainly conducted as an experiments or field observations with a notable share of in-situ experiments, while there is a scarcity of long-term biological monitoring data. This is an important gap as it limits our understanding of species recovery rates and long-term impacts. This is well illustrated by a study that showed how octocoral populations that were severely affected by the marine heatwaves in 2003 had not recovered almost two decades later [28]. Strengthening biological monitoring and aligning it with existing physical observing systems should be one of the central priorities for future Mediterranean MHW research [29]. For example, T-MEDNet [30] already provides a regional Marine Heatwave Tracker with near-real-time maps based on satellite-derived sea surface temperature, and it also includes standardised protocols for monitoring climate-related biological responses in Mediterranean coastal ecosystems. This existing physical-observation framework could be strengthened by expanding the biological component, including repeated surveys of sentinel species, population condition, recruitment, disease signs, mortality, and post-event recovery. Fisheries-independent surveys such as MEDITS [31] and MEDIAS [32] could further extend MHW monitoring towards demersal and pelagic communities. Such integration would allow biological responses to be compared across sites and events, improve detection of delayed or cumulative impacts, and provide data directly usable for marine protected area management, habitat restoration, and fisheries or aquaculture adaptation.

Taxonomic distribution of research is also uneven. Most of the studies are concentrated on the cnidarians, seagrasses and molluscs, likely because of the prior ecological research priorities

and the relative accessibility of sessile benthic organisms. For example, the dominance of cnidarians, particularly gorgonians, can be partly attributed to monitoring efforts initiated in the western Mediterranean following the mass mortality events of 1999 and 2003 [15]. These events initiated structured research into the decline of key species including *Paramuricea clavata* (Risso, 1827), *Eunicella singularis* (Esper, 1791) and *C. rubrum*, focusing on population dynamics, functional roles within coralligenous assemblages, and increasing microbiome-based approaches to understand holobiont responses to thermal stress [33, 34, 35]. Available long-term data for *E. singularis* indicate that recurrent MHWs between 2005 and 2021 have reduced population viability even within marine protected areas, suggesting that current spatial protection may not be sufficient under extreme thermal events [36]. Research on *Posidonia oceanica* has followed similar expansion. Early studies identified shoot mortality as a main response to marine heatwaves [37]. More recent work has documented biochemical responses, including changes in fatty acid composition [38]. Disruption of reproductive processes has also been reported, with mass flowering and pseudovivipary following reductions in rhizome growth over several years [39].

The uneven taxonomic distribution observed here aligns with global marine heatwave research but shows a distinct Mediterranean focus. Global reviews [40, 41] report that MHW impacts are studied across biological levels, with field studies emphasising abundance, distribution, and mortality, and laboratory work focusing on physiological and biochemical responses. Our results follow this pattern, although Mediterranean studies are strongly concentrated on benthic, habitat-forming taxa whose responses to thermal stress are directly observable through mortality and habitat degradation. This also matches global findings that marine heatwaves drive decline in coastal foundation species [41].

Although most outcomes documented in this dataset were negative, some species show signs of possible acclimation. For example, in *P. oceanica*, previous exposure to elevated temperature or local thermal history may increase resistance to future MHWs, although it remains difficult to separate true adaptation from physiological plasticity [16, 17]. Evidence from macroalgae is more limited but follows a similar direction. Laboratory experiments on *Gongolaria barbata* (Stackhouse) Kuntze, 1891 indicated potential for physiological recovery after marine heatwave exposure [42], and studies on canopy-forming species have shown acclimation potential under certain thermal conditions [43]. Among cnidarians, colony resizing has been assumed to be a plastic response of octocorals exposed to warming, although its ecological relevance in the long-term remains uncertain under the increasing frequency of marine heatwaves [44]. These examples suggest that some Mediterranean species might have limited capacity for acclimation or adaptation, but current evidence is still limited and taxon-specific.

At the trait level there was an emphasis on physiology and growth that reflects the logistics of measuring these traits in laboratory and their direct relevance to organismal fitness. In contrast, genetics, cellular responses and biochemical composition were underrepresented even though molecular-level data are essential for understanding the mechanisms behind thermal tolerance and adaptive capacity.

The limited representation of commercially relevant species indicates a mismatch between research effort and Mediterranean fisheries and aquaculture priorities. *M. galloprovincialis* received most attention, with studies covering several response traits, including physiology, genetics, cellular responses, and behaviour [45]. Field observations of mass mussel mortality recorded over three consecutive years, from 2022 to 2024, along the Italian mid-Adriatic coast show how pressing this line of work has become [21]. There is even less data on commercially important fishes: only four records were found, covering three species [46, 47, 48, 49]. Given the role of fisheries and aquaculture in the Mediterranean region, this remains a notable gap.

Current conclusions on the impacts of marine heatwaves in the Mediterranean Sea are based on sessile, habitat-forming species. Their limited capacity to avoid thermal stress may not reflect the responses of mobile or pelagic taxa. Taxonomic coverage should therefore be expanded more systematically, with particular attention to mobile species, planktonic communities, and early life stages of ecologically and commercially important taxa.

A limitation of this review is that the literature search was restricted to the Web of Science Core Collection. Although this approach ensured a consistent and reproducible screening framework, relevant studies indexed only in Scopus or other regional databases may have been omitted. Therefore, the results should be interpreted as a synthesis of Web of Science-indexed peer-reviewed literature rather than an exhaustive account of all Mediterranean marine heatwave research.

5. CONCLUSION / *Zaključak*

Marine heatwaves have moved from an emerging concern to a documented and accelerating threat to Mediterranean marine biodiversity. This synthesis shows that, even though scientific attention has increased rapidly, the evidence base remains taxonomically narrow, shaped by single-event studies, and insufficiently aligned with Mediterranean socio-economic priorities. Future monitoring frameworks should integrate biological indicators with physical MHW observations and rely on standardised long-term surveys that provide baseline, event-response, and post-event recovery data. Research should expand to include mobile and pelagic organisms, early life stages, commercially relevant species, trophic interactions, and ecosystem-level responses. Adaptive management should use these data to define risk thresholds, identify vulnerable habitats and aquaculture areas, and support potential timely responses such as targeted restoration, temporary protection measures, and site-specific aquaculture adaptation plans. Stronger integration between ecological monitoring, conservation planning, fisheries and aquaculture management, and climate adaptation policies will be necessary to translate Mediterranean marine heatwave research into practical management action.

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