Received: 22 August 2025 | Revised: 10 November 2025 | Accepted: 15 November 2025

https://doi.org/10.56946/jzs.v3i2.764

Journal of Zoology and Systematics

Review Article

Climate Change Impacts on Basking Shark (*Cetorhinus maximus*) Nutritional Status, Health, and Ecophysiology: An Integrative Systematic Review

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Abstract

Climate change presents multifaceted challenges to marine ecosystems, with particularly significant implications for large marine vertebrates such as the basking shark (Cetorhinus maximus). This systematic review examines how climate-driven alterations in ocean conditions affect the nutritional status, health, disease resilience, and related physiological processes of basking sharks, and explores the consequent impacts on their migration patterns and prey-seeking behaviours. Through comprehensive analysis of available literature, this review identifies key climate stressors including ocean warming, acidification, deoxygenation, and associated changes in zooplankton communities that form the foundation of basking shark nutrition. The findings reveal complex cascading effects from altered prey availability and quality to compromised physiological condition, bioenergetics, reduced immune function, disease risks and modified spatial ecology. These climate-mediated changes pose significant threats to basking shark populations already vulnerable due to their slow life history characteristics and limited genetic diversity.

Keywords: Basking shark, climate change, nutritional ecology, bioenergetics, zooplankton, ecophysiology, migration

1. Introduction

The basking shark (Cetorhinus maximus) represents the world's second-largest fish species and serves as a critical indicator of marine ecosystem health [1]. Basking sharks are obligate planktivores and primarily consume copepods for their nutritional requirements [2]. Their specialised feeding strategy makes basking sharks particularly vulnerable to climate-driven changes in marine food webs, as their survival depends on the availability, distribution, and nutritional quality of microscopic prey organisms [3] and as depicted in Figure 1.

Climate change is fundamentally altering ocean conditions through multiple interconnected mechanisms. Ocean temperatures have risen by over 1.5°C since the Industrial Revolution, with marine organisms experiencing narrow thermal safety margins that leave little room for adaptation [4]. Simultaneously, increased atmospheric CO_2 absorption by oceans is driving acidification and deoxygenation processes that further compound environmental stressors [5]. These changes are particularly pronounced in the temperate and boreal waters that basking sharks typically inhabit, creating unprecedented challenges for species adapted to relatively stable oceanographic conditions [6].

The consequences of climate change extend beyond simple temperature increases to encompass complex reorganisation of marine food webs. Zooplankton communities, which form the base of basking shark nutrition, are experiencing dramatic shifts in species composition, phenology, and nutritional quality [7,8].

Figure 1. A near surface, grazing adult Basking shark (Cetorhinus maximus) (Image source *Simon J Davies*).

Evidence suggests that climate-driven changes in copepod communities can reduce essential fatty acid availability by up to 30%, with cascading effects throughout marine food chains [9]. For basking sharks, these changes in prey quality and availability may fundamentally alter their energy budgets, health status, and survival prospects.

Recent discoveries have revealed that basking sharks possess regional endothermic capabilities similar to apex predatory sharks, challenging previous assumptions about their thermal physiology [10]. This finding has important implications for understanding their responses to ocean warming and the energetic costs associated with thermoregulation in a changing climate. Furthermore, basking sharks demonstrate complex migration patterns that may be disrupted by climate-driven shifts in prey distribution and ocean currents [11].

This systematic review synthesises current knowledge on climate change impacts on basking shark biology, with particular focus on nutritional status, health, and bioenergetics. We examine the mechanisms through which climate change affects prey availability and quality, analyse the physiological consequences for basking shark health and immune function, and explore how these changes influence migration patterns and foraging behaviour.

2. Methods

2.1. Search Strategy

A comprehensive systematic literature search was conducted across multiple electronic databases including Web of Science, Scopus, PubMed, and Google Scholar for the period 1990-2025. Search terms included combinations of "basking shark," "*Cetorhinus maximus*," "climate change," "ocean warming," "acidification," "zooplankton," "copepods," "nutrition," "bioenergetics," "migration," "health," and "disease." Additional searches targeted specific topics such as "marine megafauna climate impacts" and "plankton climate change effects." This was undertaken by application of Claude Sonnet

4.5, Gemini 2.5 Pro and Grok 4 deep search with prompts for each area of interests for an integrative strategic platform.

2.2. Inclusion and exclusion criteria

Studies were included if they: [1] contained original research or comprehensive reviews relevant to basking shark biology or marine ecosystems; [2] addressed climate change impacts on marine organisms, particularly filter-feeding species or zooplankton; [3] examined nutritional ecology, bioenergetics, or health aspects of marine vertebrates; [4] investigated climate-driven changes in marine food webs; and [5] were published in peer-reviewed journals or authoritative reports. Comprehensive reviews were screened prior to selection to avoid repetitive data acquisition and avoid selection bias by cross-checks that included studies against previous meta-analyses and systematic reviews to identify potential doubled data and confirm unique datasets. Assistance by external associates was provided to employ specialized systematic review platforms [Covidence, Rayyan, Ovid] to enhance de-duplication accuracy and collaboratively screen studies. Only documented and peer-reviewed publications with validated Doi's were considered in this review article. Initial database search: 395 citations screened for title and abstract screening: 128 excluded, 267 proceeded to full-text review. Full-text review: 201 excluded, 66 included in the final review and meta-analysis. The flow chart (Figure 2) presents the selection and rejection criteria and summation of citations used in the synthesis of the review.

2.3. Reasons for exclusion included

Studies not related to basking sharks or relevant marine species,

- Papers focused on unrelated animal groups, ecosystems, or unrelated climate/trophic variables,
- Non-peer reviewed sources [unless authoritative reports],
- Duplicate records,
- Incomplete, inaccessible, or non-English manuscripts [if no translation or abstract in English was available].

2.4. Data Extraction and Analysis

Data were extracted from eligible studies and categorised into themes including: [1] climate stressors and oceanographic changes; [2] zooplankton community responses; [3] nutritional and bioenergetic impacts; [4] health and disease implications; and [5] behavioural and migration responses. Results were synthesised narratively, with particular attention to mechanisms and cascading effects relevant to basking shark ecology.

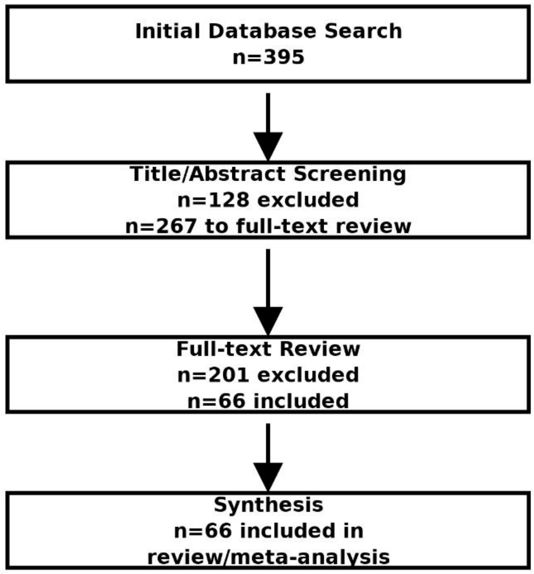

Figure 2. Flowchart of citation screening and inclusion/ exclusion in the systematic review on basking sharks and climate change effects

3. Findings and Discussion

3.1. Ocean Warming

Ocean warming represents the most pervasive climate stressor affecting basking shark habitats. Surface temperatures in temperate waters have increased significantly, with the North Atlantic showing warming rates of up to 2°C during the recent decades [12]. Basking sharks typically occupy waters between 8-16°C in the Northeast Atlantic, but rising temperatures are expanding these thermal envelopes and altering the spatial distribution of suitable habitat zones [13].

The thermal tolerance of basking sharks has been traditionally considered relatively narrow, but recent research reveals greater flexibility than previously assumed for this species [14], demonstrating significant behavioural plasticity within its realised thermal niche [15]. Individuals that travelled offshore and into further southern latitudes off Africa, showed a distinct daily cycle of deep dives [00:00–12:00, 200 m–700 m; 12:00–00:00, 0–300 m], undergoing more extreme ranges of temperatures from 6.8–27.4 °C, including cooler minimum temperatures, than those remaining in European coastal habitat typically around 9.2–17.6 °C. However, this thermal flexibility comes with energetic costs, as metabolic rates increase exponentially with temperature, potentially requiring 2-3 times greater energy expenditure in warmer waters [16].

3.2. Ocean Acidification

Ocean acidification poses both direct and indirect threats to basking sharks. While sharks possess acid-base regulatory mechanisms, prolonged exposure to reduced pH conditions can compromise physiological function [17]. More significantly, acidification affects the zooplankton communities that form the base of basking shark food prey and nutrition. Ocean pH has declined by ~ 0.1 since pre-industrial times, with significant impacts on calcifying plankton species [18]. Experimental studies demonstrate that sharks exposed to projected future pH levels may incur impaired olfactory function, which would compromise their ability to locate productive feeding areas [19]. Additionally, acidification appears to cause physical damage to shark dermal denticles, potentially affecting swimming efficiency and increasing energy costs [20].

3.3. Deoxygenation

Climate-induced deoxygenation represents an emerging threat to basking shark populations. Warmer waters hold less dissolved oxygen, while increased stratification reduces vertical mixing that replenishes surface oxygen levels [21]. Hypoxic conditions can directly impact shark survival, with experimental studies showing 31% mortality increases in embryonic sharks exposed to low-oxygen environments under controlled laboratory conditions of exposure where it was observed early ontogenetic acclimation process of a tropical shark [*Chiloscyllium punctatum*] to the projected scenarios of further ocean acidification [ΔpH = 0.5] and warming [+ 1.2-3.2°C] possibly by the turn of the century at 2100. These studies validated significant impairments on juvenile shark condition and survival under such circumstances [22]. The deoxygenation process also affects prey communities, with many copepod species showing reduced reproductive success and altered vertical migration patterns under hypoxic conditions [23]. This indirect effect may be more significant for basking sharks than direct physiological impacts, as it fundamentally alters the distribution and availability of their major prey.

3.4. Zooplankton Community Responses to Climate Change

3.4.1. Phenological Shifts

Climate warming is causing dramatic shifts in zooplankton phenology, with timing changes of 5-10 days per decade observed across multiple species [24]. These shifts are particularly pronounced in copepods, which show earlier spring emergence and compressed seasonal windows of peak abundance [25]. Specific studies have quantified the advancement relative to warming and report faster development and earlier spawning during warm years compared to cold years. This directly linking local temperature increases to phenological shifts and abundance [26].

For basking sharks, these phenological mismatches pose significant challenges. The species has evolved to time migrations and feeding behaviour to coincide with peak zooplankton abundance [27]. However, if shark movements cannot adapt quickly enough to match shifting prey phenology, this could result in reduced feeding opportunities and compromised nutritional status.

3.4.2. Species Composition Changes

Climate change is driving fundamental reorganisation of zooplankton communities. Cold-water copepod species are being replaced by smaller, warm-water species with lower lipid content and reduced nutritional value due to changes in fatty acid profiles [28]. Large diapausing copepods that are crucial for marine megafauna nutrition are showing significant habitat losses, with some species projected to lose 40-60% of suitable habitat by 2100 [29]. In many regions, high-quality zooplankton species are being replaced by smaller organisms such as the cyanobacterium *Synechococcus*, which lacks essential biomolecules and cannot sustain marine food webs efficiently [30]. This shift toward smaller, less nutritious plankton represents a fundamental degradation in food web productivity that could have severe consequences for filter-feeding megafauna.

3.4.3. Nutritional Quality Decline

The nutritional quality of zooplankton is declining under climate change through multiple mechanisms. Essential fatty acids [EPA and DHA] in copepods decrease by approximately 6% per degree of warming, with some studies showing reductions of up to 30% in essential lipid content [31,32]. These fatty acids are crucial for marine predator health, supporting immune function, reproduction, and cellular membrane integrity. Temperature also affects lipid storage patterns in copepods. Under thermal stress, copepods show compromised ability to utilise storage fatty acids as energy sources, potentially reducing their caloric value as prey [33]. This effect is compounded by changes in phytoplankton communities, as nutrient-limited conditions reduce the essential fatty acid content of primary producers [34].

3.5. Nutritional and Bioenergetic Impacts on Basking Sharks

3.5.1. Energy Budget Alterations

Climate change is fundamentally altering basking shark energy budgets through both increased metabolic demands and reduced prey quality. The discovery that basking sharks are regional endotherms similar to white sharks has important implications for their energetic responses to warming waters [35]. Maintaining elevated body temperatures in warmer environments requires additional energy expenditure, potentially increasing metabolic costs by 15-25% in projected future conditions [36].

Basking sharks exhibit threshold foraging behaviour, ceasing feeding when prey densities drop below levels that provide net energetic gain [37]. Current estimates suggest basking sharks require oxygen consumption rates of 80.7 mg O_2 $kg^{-}1$ h^{-1} for a 5-meter individual, with feeding thresholds around 0.62 g wet weight m^{-3} of zooplankton but studies show a range from 52.0 to 99.2 mg O_2 $kg^{-}1$ h^{-1} depending on body mass, filter-feeding activity, and environmental conditions [38]. As climate change reduces prey quality and density, sharks may increasingly encounter conditions below these recorded feeding thresholds. The energetic cost of breaching behaviour, which may serve social or parasite removal functions, represents approximately 1/17th of daily metabolic requirements for basking sharks [39]. Under increased metabolic stress from climate change, the relative cost of such behaviours may become prohibitive, potentially affecting social interactions and health maintenance.

3.5.2. Physiological Stress Responses

Climate stressors activate complex physiological stress responses in sharks that can compromise health and immune function. The oxygen and capacity-limited thermal tolerance [OCLTT] concept suggests that warming beyond optimal thermal ranges reduces aerobic scope and performance capacity in marine animals [40]. This framework predicts that basking sharks in warming waters will experience reduced fitness and increased vulnerability to additional stressors.

Experimental studies on other shark species demonstrate that combined warming and acidification can reduce survival by up to 44% in early life stages as shown for the tropical shark species, *Chiloscyllium punctatum* [41]. While direct experimental data for basking sharks are limited due to their size and conservation status, related species show compromised immune function, reduced growth rates, and increased mortality under projected climate conditions [42].

3.6. Health and Disease Implications

3.6.1. Immune System Competence

Climate change poses significant threats to basking shark immune function through multiple pathways. Temperature stress is the primary driver of immune system dysfunction in fish, with temperatures outside optimal ranges suppressing both innate and adaptive immune responses [43]. Experimental studies on temperate sharks show that marine heatwaves reduce immune gene expression and alter cellular immunity, potentially increasing disease susceptibility [44].

Ocean acidification compounds these effects by disrupting acid-base balance and cellular function. Combined warming and acidification appear to have synergistic negative effects on shark physiology, with the interaction between stressors more damaging than either factor alone [45]. Hypoxic conditions further compromise immune function, with studies showing reduced immunocompetence in sharks exposed to low-oxygen environments [46].

3.6.2. Disease Susceptibility

While few diseases have been documented in basking sharks historically, climate change may increase vulnerability to pathogens [47]. Warming temperatures facilitate pathogen growth and transmission, while environmental stress compromises host defence mechanisms at both physiological and metabolic systemic levels. In the most common case, specific documented disease in basking sharks includes chronic skin disease with copepod ectoparasites that may be seasonal in nature but potentially linked to environmental stressors [48]. In fact, oceanic heatwaves have been linked to increased disease outbreaks and mass mortality events in marine megafauna globally in recent years, including sharks and rays. Recently, this has prompted considerations of the skin and microbial barrier to shark health and disease resistance as a promising new field of research [49].

Both the integument and gut microbiota is now becoming an important avenue for research in shark biology in relation to disease susceptibility and fitness. Actually, the first documented case of disease in a basking shark was in 2010 and involved pyogranulomatous meningoencephalitis and dermatitis, possibly of bacterial origin [50]. While this case predates contemporary major climate impacts, the inflammatory nature of the pathology suggests that stressed individuals might be more susceptible to similar infections under future climate conditions. The case in question [50] described the clinical signs and gross and microscopical pathology in a diseased basking shark that was live stranded on the east coast of Scotland. *Pyogranulomatous* meningoencephalitis appeared to be the causative agent together with multifocal, mainly non-suppurative, myocarditis with myocyte (contractile muscle cell) necrosis, oedema and haemorrhage of major tissues, organs and skin.

3.6.3. Parasite Dynamics

Climate change may alter parasite-host dynamics in basking sharks through several mechanisms. Warming temperatures can accelerate parasite development and increase transmission rates, while stress compromises host resistance [51]. Interestingly, some parasites may provide benefits by sequestering heavy metals and toxins from shark tissues, potentially offering protection against pollution-related stress. The mechanism of action relates to the absorption of certain types of toxins and their metabolites reducing availability for sharks [52]. This would present a conundrum in the management of basking shark populations if such scenarios prevailed. As such, changes in basking shark distribution and migration patterns due to climate change could expose populations to novel parasite assemblages or disrupt co-evolved host-parasite relationships [53]. The complex relationship between grouping behaviour and parasitic pressure in sharks suggests that climate-driven changes in social behaviour could also affect parasite loads, leading to deleterious situations [54].

3.7. Migration and Foraging Behaviour Responses

3.7.1. Altered Migration Patterns

Climate change is disrupting basking shark migration patterns through multiple interacting mechanisms. Ocean warming is causing poleward shifts in suitable habitat, with species distributions moving northeast at rates of approximately 35 km per decade [55]. This range shift forces sharks to undertake longer migrations to reach suitable feeding areas, increasing energetic costs and exposure to additional anthropogenic threats.

Recent research reveals that basking shark migration strategies are more complex than previously understood. Some individuals remain in northern waters year-round, while others migrate to tropical waters where they undergo dramatic vertical movements to access deep, cold waters [56]. These diverse strategies may represent adaptations to changing ocean conditions, but they also increase the challenges of conservation management. The timing of migration is also shifting in response to changing prey phenology. Some coastal shark species now delay southward migrations by up to 29 days due to warming waters, remaining in northern habitats longer [57]. For basking sharks, such timing shifts could affect breeding cycles, energy allocation, and exposure to seasonal stressors.

3.7.2. Foraging Efficiency Changes

Climate-driven changes in prey distribution and quality are affecting basking shark foraging efficiency. The species shows selective feeding behaviour, concentrating efforts in areas with high densities of large calanoid copepods near thermal fronts [58]. As these productive frontal zones shift or weaken due to climate change, sharks must modify their foraging strategies or accept reduced feeding success. The breakdown of synchrony between shark arrival and peak prey abundance due to phenological mismatches may force sharks to exploit suboptimal feeding areas or extend foraging periods [59]. This could increase energetic costs while reducing nutritional gains, creating an increasingly unfavourable energy balance.

3.7.3. Habitat Quality Degradation

Climate change is degrading the quality of basking shark habitats through multiple pathways. Rising sea surface temperatures are expanding oligotrophic "ocean desert" areas where primary productivity is low [60]. Simultaneously, the breakdown of thermal stratification patterns is reducing the predictability of productive feeding areas that sharks have historically relied upon [61]. Such changes could be a major disrupter in basking shark habitat and physiology with serious consequences. In fact, species distribution models predict significant habitat shifts for basking sharks under future climate scenarios, with suitable habitat moving toward higher latitudes and deeper waters [61]. While this might provide refugia in some regions, it also fragments populations and increases the energetic costs of accessing suitable habitat.

3.8. Population-Level Consequences and Conservation Implications

3.8.1. Genetic Vulnerability

Basking sharks exhibit exceptionally low genetic diversity, with whole mitogenome analyses revealing nucleotide diversity of only 0.0005 [62]. This low diversity, combined with small effective population sizes, makes the species particularly vulnerable to environmental changes and reduces adaptive potential [63]. Climate change may exacerbate these genetic constraints by reducing population connectivity and increasing local extinction risks. The species' slow life history characteristics including late maturation [16-20 years], long gestation periods [2.6-3.5 years], and low fecundity, limit population recovery potential [64]. These traits make basking sharks especially vulnerable to climate-driven mortality increases, as populations cannot quickly replace losses or adapt to changing conditions.

3.8.2. Cumulative Stress Effects

Climate change impacts on basking sharks do not occur in isolation but interact with other anthropogenic stressors. Entanglement in fishing gear, vessel strikes, and habitat degradation all increase under climate-driven changes in shark distribution and human activities [65]. The combination of nutritional stress, compromised immune function, and increased anthropogenic threats creates a syndrome of cumulative impacts that may exceed the species' capacity for resilience. One important point to consider is that marine protected areas [MPAs] established for basking shark conservation may become ineffective as climate change shifts suitable habitat zones outside protected boundaries [66]. This highlights the need for adaptive management strategies that can respond to changing species distributions and habitat requirements.

3.9. Synthesis and Future Directions

The evidence reviewed reveals a complex web of climate change impacts on basking shark biology, with cascading effects from altered ocean conditions through zooplankton communities to individual shark health and population dynamics. The key pathways identified include:

1. **Direct physiological stress** from warming, acidification, and deoxygenation
2. **Prey base degradation** through zooplankton community shifts and nutritional quality decline
3. **Bioenergetic compromise** due to increased metabolic demands and reduced food quality

4. **Immune system dysfunction** leading to increased disease susceptibility
5. **Behavioural disruption** affects migration timing and foraging efficiency

These impacts interact synergistically, with the potential for threshold effects that could trigger rapid population declines. The recent discovery of basking shark endothermy adds complexity to our understanding of their thermal responses and suggests that metabolic costs of climate adaptation may be higher than previously estimated.

Critical knowledge gaps remain, particularly regarding direct experimental studies of climate impacts on basking sharks. The species' size, conservation status, and oceanic lifestyle make controlled experiments challenging, necessitating innovative approaches such as physiological modelling and comparative studies with related species.

Future research priorities should include the following criteria:

1. long-term monitoring of basking shark body condition and health.
2. Investigation of adaptive capacity and phenotypic plasticity.
3. development of bioenergetic models incorporating climate variables.
4. Assessment of prey quality changes in key feeding areas
5. Evaluation of conservation strategies under projected climate scenarios.

4. Conclusions

Climate change represents a multifaceted threat to basking shark populations through mechanisms that span from molecular to ecosystem levels. The degradation of zooplankton prey quality and availability, combined with increased physiological stress and reduced immune function, creates conditions that may exceed the adaptive capacity of this slow-growing, low-diversity species. The complex migration patterns and habitat requirements of basking sharks make them particularly vulnerable to climate-driven oceanographic changes.

Conservation efforts must evolve to address these climate impacts through adaptive management strategies that account for shifting habitat suitability and changing environmental conditions. The maintenance of productive marine ecosystems and zooplankton communities will be essential for basking shark survival, highlighting the need for broader climate mitigation efforts alongside species-specific conservation measures. The case of the basking shark illustrates the far-reaching consequences of climate change for marine megafauna and underscores the urgency of addressing both climate drivers and ecosystem-level impacts to preserve these magnificent ocean giants for future generations.

Author contributions

Simon J. Davies: Conceptualization; Methodology; Investigation; Data curation; Formal analysis; Writing – original draft; Writing – review & editing; Visualization; Project administration.

Ethical approval

Approval was not required for this scientific based literature review

Conflicts of Interest

The author reports no conflicts of interest.

Acknowledgment

The author acknowledges the external advisory support of Matt E. Bell and Paul Van Der Heijden for guidance on literature search refinement and risk-of-bias assessment. They were not involved in authorship or decision-making in the review process.

Data availability statement

This review is based on published literature cited in the selected references. No original experimental data was generated for this work by the author.

Funding

No specific funding was received or necessary for this review.

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How to cite this article: Davies, S. J. (2025). Climate Change Impacts on Basking Shark (*Cetorhinus maximus*) Nutritional Status, Health, and Ecophysiology: An Integrative Systematic Review. Journal of Zoology and Systematics, 3(2), 133–144.