2023-10

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https://pearl.plymouth.ac.uk/handle/10026.1/21697

10.1016/j.ecoser.2023.101542
Ecosystem Services
Elsevier BV

Ecosystem Services 63 (2023) 101542

Contents lists available at ScienceDirect

Ecosystem Services

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

Review Paper

An assessment of the ecosystem services of marine zooplankton and the key threats to their provision

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ARTICLE INFO

Keywords:
Copepods
Krill
Jellyfish
Climate change
Fisheries
Microplastics

ABSTRACT

Zooplankton are a key group of organisms at the base of the marine food web and are fundamental to providing a broad range of societal and economic benefits which have previously remained poorly defined. This research addresses this knowledge gap through the provision of a first full assessment of zooplankton ecosystem services and disservices. Anthropogenic stressors such as microplastic pollution, climate change, and fisheries, could negatively affect the marine ecosystem services provided to humans and therefore have a negative impact on human well-being through reduction in food security, livelihoods, income, and good health. Deploying a mixed methodology approach including a semi-systematic literature review and ecological impact assessment, we provide novel evidence of the effects of microplastic pollution (high and low concentrations), fisheries, and climate change on the ecosystem services of three important zooplankton groups (copepods, jellyfish, and krill). We show that the majority of impacts on ecosystem services are negative, with the exception of climate change on jellyfish ecosystem services. Climate change and high microplastic concentration are evidenced to have the most substantial negative impacts on copepods and krill, with accompanying implications for the ecosystem services of climate regulation, water conditions, other materials, science, and entertainment. High microplastic concentration also depressed ecosystem service provision for jellyfish, impacting the services of genetic materials, climate regulation, water conditions, education, and entertainment. Fisheries are also evidenced to have negative impacts on all three zooplankton groups. In the case of jellyfish, climate change is evidenced to have a positive impact on the group's ecosystem service provision in every category except experiential experiences, which is inversely related to increasing population, owing to their negative perception due to sting injuries. The evidence presented in this study shows that by maintaining sustainable fisheries, reducing plastic pollution, and minimising climate change, we will be actively investing in the current and future provision of marine ecosystem services and the human well-being benefits that they provide.

1. Introduction

Marine ecosystems provide a multitude of ecosystem services (benefits people obtain from nature) which include food, carbon storage, oxygen production and recreation (Worm et al., 2006; Liquete et al., 2013). However due to unsustainable anthropogenic activities and ineffective ecosystem management, these ecosystem services are under pressure globally. Any stressor that may affect the ecosystem services provided to humans, could have a negative impact on human well-being through reduction in food security, livelihoods, income, and good health (Naeem et al., 2016; Beaumont et al., 2019).

Previous studies have reported the ecosystem services of habitats (salt marshes (Rendón et al., 2019)), ecosystems (Southern Ocean (Grant et al., 2013)), groups of marine animals (mammals (Riisager-Simonsen et al., 2020), jellyfish (Doyle et al., 2014; Graham et al., 2014)) and how anthropogenic stressors such as plastic pollution may impact ecosystem services (Beaumont et al., 2019). So far, in-depth ecosystem service assessments on marine fauna have focussed on species that are either charismatic (e.g., marine mammals) or problematic (e.g., jellyfish). Yet zooplankton, a key group of organisms which underpin marine food

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https://doi.org/10.1016/j.ecoser.2023.101542
Received 19 May 2022; Received in revised form 25 May 2023; Accepted 5 July 2023

webs, aid nutrient cycling and carbon sequestration have only been partially assessed (Doyle et al., 2014; Graham et al., 2014; Lomartire *et al.*, 2021). Zooplankton are critical to the health and functioning of marine ecosystems and as a result provide numerous ecosystem services with accompanying implications for human well-being.

There are many stressors that zooplankton face in the marine environment, including eutrophication (Marcus, 2009), climate change (McGinty et al., 2021), invasive species (Dexter & Bollens, 2020), microplastic pollution (Cole et al., 2013; Botterell et al., 2019), chemical and oil pollution (Hernández Ruiz et al., 2021; Sørensen et al., 2023), overexploitation by fisheries (Nicol & Foster, 2016) and anthropogenic noise (McCauley et al., 2017). Of these microplastic pollution has been listed as an environmental contaminant of emerging and legacy concern by several global regulatory bodies (GES, Subgroup & Litter, 2011; OSPAR, 2014; UNEP, 2017, SAPEA, 2020). Subsequently there exists extensive research conducted in this area using zooplankton that could be translated into ecosystem service impacts. Additionally, there is plentiful available literature on another chronic stressor, climate change, and an acute stressor, fisheries, in which ecosystem service impact could also be investigated and compared.

Climate change, due to the continued burning of fossil fuels and subsequent rise in carbon dioxide levels, has led to increases in global temperatures and ocean acidification, therefore altering the environment in which zooplankton inhabit. Scenario RCP 4.5 indicates that there is likely to be a 2–3 °C of warming by the end of this century and a 38–41% increase in acidity of the ocean surface, which will have a worldwide effect (IPCC, 2014). Implications for zooplankton include changes to species ranges (Chivers et al., 2017; McGinty et al., 2021, Smith et al., 2016), reduction in food availability (Flores et al., 2012), and impacts to reproduction (Wang et al., 2018; Treible and Condon, 2019; Perry et al., 2020). It has been estimated that 4.8–12.7 million tonnes of plastic pollution entered the marine environment from land-based sources in 2010, this has been predicated to increase by an order of magnitude by 2025 (Jambeck et al., 2015). The small size of many species in the zooplankton means that microplastics often overlap with the size of their prey (Botterell et al., 2019). Zooplankton are also found in areas of high productivity such as coastal areas which also have high microplastic concentrations due to inputs from land-based sources (Clark et al., 2016). Microplastics impact zooplankton by negatively affecting their feeding behaviour, growth/development and reproduction (Lee et al., 2013; Cole et al., 2015; Bergami et al., 2016; Costa et al., 2020). Finally, there are valuable fisheries of krill and jellyfish, and an emerging fishery for copepods (CCAMLR, 2021; FAO, 2021; Zooca, 2021). Unlike climate change and microplastic pollution, fisheries are not a chronic exposure and each catch immediately decreases the population size. These fisheries therefore need to be sustainably managed to prevent over harvesting of the zooplankton.

It is clear that these global stressors will have an effect on zooplankton and therefore impact their ecosystem services. To date there has been no previous assessment of how fisheries may impact the ecosystem services of zooplankton, and there has only been limited publications of how climate change may decrease the services of the krill fishery in the Southern Ocean (Grant et al., 2013; Cavanagh et al., 2021), but does not assess the further services that krill provide. Whilst previous research has predicted a reduction in ecosystem service provision by most marine animal groups including zooplankton (assessed as a whole group) due to plastic pollution (Beaumont et al., 2019), zooplankton are a broad and diverse group of organisms which includes, but is not limited to, mixotrophic dinoflagellates, copepods, larvae of shell- and finfish, krill, and jellyfish. This therefore requires a more in-depth analysis to determine if the ecosystem services from the different zooplankton will be affected in the same way or if there is within group variation. This understanding is essential for future decision making at regional and global levels where zooplankton populations could be impacted i.e., the importance of krill in Antarctica and copepods in the Arctic. It may also indicate future problematic scenarios (i.e., jellyfish blooms) that may require high costs to remediate, for example due to development of technology (i.e., removal from power plants) and/or healthcare (i.e., treatment costs).

In this study we: 1) describe the ecosystem services and disservices of zooplankton (section 3.1 and 3.2), 2) conduct an ecological impact synthesis of three stressors: climate change, microplastic pollution (low and high concentrations) and fisheries, on three groups within the zooplankton (copepods, jellyfish, and krill) (section 3.3) and 3) translate these ecological impacts into ecosystem service impacts for each zooplankton group, for each anthropogenic stressor (section 3.3). The findings are then brought together to formulate discussion and make recommendations for the future.

2. Methods

2.1. Assessment of ecosystem services and disservices from marine zooplankton

There are numerous ecosystem services frameworks, including the Millennium Ecosystem Assessment (MA, 2005), The Economics of Ecosystem Biodiversity (TEEB, 2010) and Common International Classification of Ecosystem Services of the European Environment Agency (CICES, 2018). Building on these frameworks and other recent studies (Beaumont et al., 2019; Riisager-Simonsen et al., 2020), we developed a framework of ecosystem services and disservices of marine zooplankton. We included both services (functions or properties of ecosystems that benefit and contribute to human well-being) (Costanza et al., 1997; Liquete et al., 2013) and disservices (functions or properties of ecosystems that have undesired effects on human well-being) (Lyytimäki and Sipilä, 2009; Dunn, 2010) because both are important in understanding the wider implications of any management investments into ecosystem services/disservices so that they may yield the best outcomes for human wellbeing (Dunn, 2010; Graham et al., 2014; Rendón et al., 2019; Riisager-Simonsen et al., 2020).

Whilst several studies have been published on the ecosystem services of jellyfish (Doyle et al., 2014; Graham et al., 2014), there is very little literature on other types of organisms which are common components of the zooplankton, with only one published study (Lomartire *et al.*, 2021). Given the minimal amount of related literature it was not possible to undertake a fully systematic review, and as such we elected to undertake a semi-systematic review of the ecosystem services of zooplankton, enabling the inclusion of the broadest evidence base.

By using the CICES ecosystem services classification, we drew up a list of potential ecosystem services (provisioning, regulating and cultural), to which we added supporting services, as recommended in the Millennium Assessment (MA, 2005). Supporting services are not included in all frameworks to avoid double counting if services are valued monetarily. However, as zooplankton provide several substantial supporting services, these have been included for reasons of completeness and to ensure the full services of zooplankton are communicated. We also include disservices, recognising that there are potential detrimental effects from interacting with nature (Rendón et al., 2019). In comparison to ecosystem services, disservices have received very little attention despite their potential to negatively impact human well-being. We therefore used frameworks within the literature (Lyytimäki and Sipilä, 2009; Shackleton et al., 2016; Rendón et al., 2019) to help inform of potential ecosystem disservices. Search terms for the review were selected from the ecosystem services terms as defined by CICES and MA, additionally keywords related to zooplankton such as 'marine zooplankton', 'copepod', 'jellyfish' and 'krill' were also used (Supplementary materials Table **S1**). These three groups of zooplankton were selected as they are dominant, keystone organisms within the zooplankton and widely researched. We searched the literature using Google Scholar and Web of Science and all relevant publications relating to ecosystem services/disservices and the selected zooplankton groups were investigated. The first 500 results of each keyword search combination were reviewed, with results rarely relevant after the first 50. Spurious (i.e., false) hits were ignored and all relevant references from within publications were recorded and investigated. All publications deemed irrelevant were first reviewed and then disregarded. Due to the limited pertinent literature (e.g., ecosystem service assessments, reviews, and studies), the examples we highlight are not an exhaustive list, but are considered indicative of ecosystem service provision by zooplankton.

2.2. *Ecological impact synthesis of anthropogenic stressors and translation into ecosystem services impact*

Following an adapted methodology by (Beaumont et al., 2019), we conducted an ecological impact synthesis of four anthropogenic stressors (low microplastic concentration, high microplastic concentration, fisheries, and climate change) on three ecologically important groups within the zooplankton; copepods, krill, and jellyfish. We use the three main ecosystem services groups as recommended by CICES in this assessment as supporting services are very broad, often overlap with other services, and could cause double counting (if monetary value is involved). Firstly, using a similar semi-systematic review methodology to the ecosystem services assessment (substituting the ecosystem services search terms for the relevant anthropogenic stressor search terms (**Supplementary materials Table S1**)), we identified relevant published literature that provided evidence of impact from the anthropogenic stressor on each zooplankton group. This evidence was systematically scored based on whether it was a positive or negative interaction, the extent of the impact (1–5), and the frequency of the impact (%) occurring in the population (1–5) which also included a traffic light confidence assessment (**Supplementary materials S2.1**). Impact is defined as an effect on energy budget, growth/development, reproductive potential and/or life span.

Then each zooplankton group was scored on its potential for providing each ecosystem service using previous global assessments and ecosystem services reviews as a guide to the scoring process, using the evidence gathered in 2.1 to assign the scores (Groot et al., 2012; Costanza et al., 2014; Beaumont et al., 2019) (**Supplementary materials S2.2**). They were scored using similar criteria as above: a positive or negative interaction (negative interaction indicating a disservice), the extent of the ecosystem service provision (1–5), and the frequency of the ecosystem service provision (1–5). This assessment was then combined with the ecological impact results (through the process of multiplication) to determine the impact of low microplastic concentration, high microplastic concentration, fisheries, and climate change on the ecosystem services of copepods, krill, and jellyfish. Scores range between +100 to −100, so a negative impact of a stressor multiplied by a negative disservice, could result in a positive benefit to human wellbeing.

Beaumont et al., (2019), conducted the same methodology as above to investigate the impact of marine plastic on several groups of marine organisms, but also included an 'extent of reversibility' category for the first ecological impact score and scored all the categories (for both ecological impact score and ecosystem service score) 1–3. We adapted this method by expanding the scoring to be between 1 and 5, to improve the specificity. We removed the reversibility category as it is unknown over what time scales the impacts due to threats investigated may be reversible, if ever, it would therefore not add a meaningful contribution to the scoring process.

2.3. *Definition of scenarios*

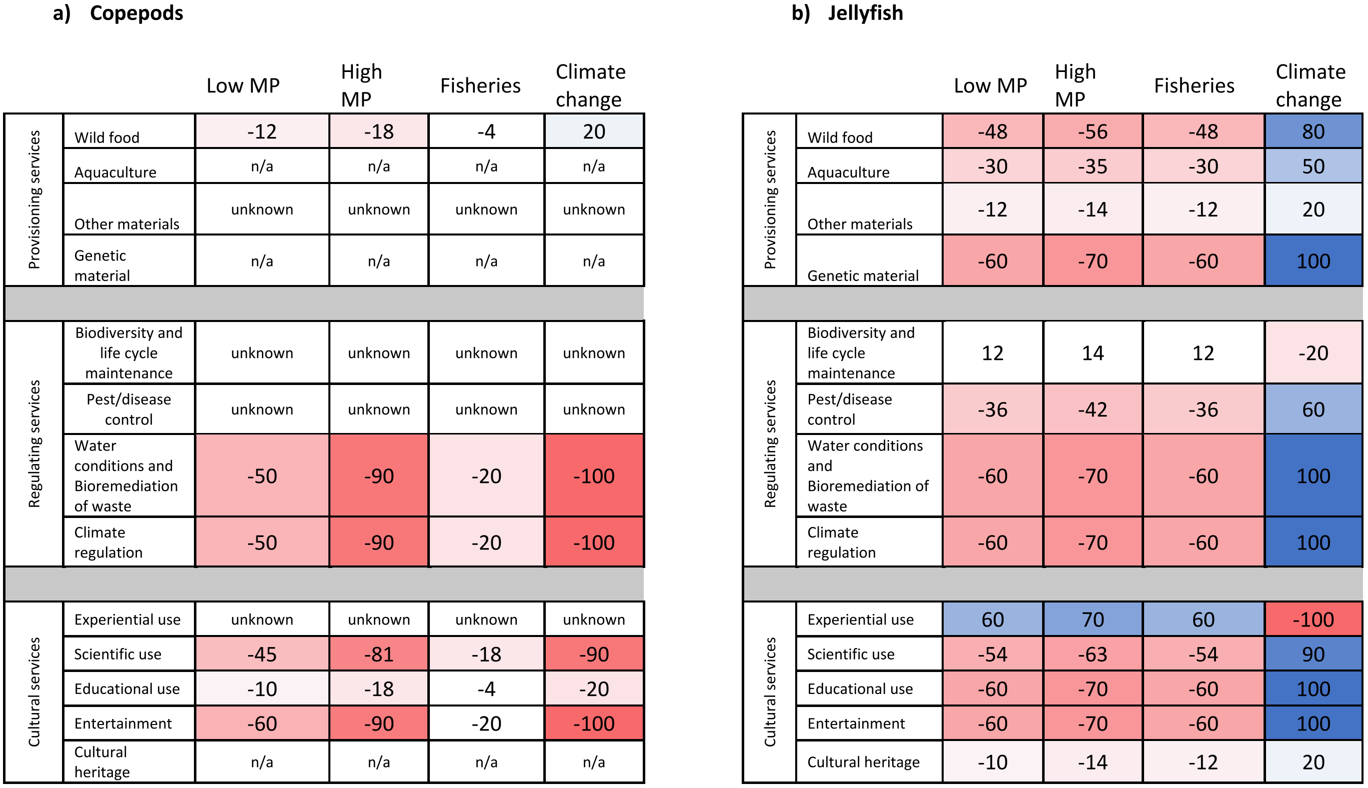
We conducted an impact analysis of microplastics, fisheries, and climate change on the ecosystem services of copepods, jellyfish, and krill (Fig. 1). These environmental stressors were chosen as they are already a notable or emerging threat to this group of marine organisms. We explore four different future scenarios: 1) An RCP 4.5 of warming to 2–3 °C and a 38–41% increase in acidity of the ocean surface; 2) a large increase in microplastics in the marine environment; 3) no increases in microplastics in the marine environment; and 4) a no change fisheries scenario based on current fishing intensity. For all scenarios we are visioning a future marine state and what this would mean for ecosystem services. This type of visioning exercise means we can think strategically about the management of our marine resources, and where we should be investing our efforts to achieve the future that best serves humanity and maximises well-being.

To explicitly define the stressors for our analysis, we used the RCP 4.5 scenario for climate change, this scenario estimates a 2–3 °C of warming by the end of the century and a 38–41% increase in acidity of the ocean surface (IPCC, 2014). We used fisheries landings and governmental quotas combined with management strategies to inform frequency of impacts (Marine Resources Act, 2008; CCAMLR, 2021; FAO, 2021). It is estimated that the krill quota data is currently set at 1% available biomass (CCAMLR, 2021) and the Calanus quota is set at $< 1\%$ of the available biomass (Marine Resources Act, 2008, Zooca, 2021). These are based on estimated population densities, unfortunately there is no estimates for the jellyfish, due to their boom-and-bust nature of their blooms, and lack of records. We therefore treated this as an opportunistic fishery where jellyfish are caught during high population densities (e.g., jellyfish blooms). For microplastic pollution we investigated two different scenarios, a low (no increase) and a high (large increase) microplastic concentration as microplastic concentrations will continue to increase in the future due to further inputs of plastic pollution and fragmentation of larger plastic already present in the marine environment. We used the current range of microplastics found in the marine environment as our low (no increase) microplastic scenario. However due to limitations in size detection of instruments and sampling methodology i.e., net mesh size, it is likely that these values are an underestimate. Additionally, recent research has shown that smaller microplastics are often found at higher concentrations (Lindeque et al., 2020). Understanding future microplastic concentrations is complex, with multiple sources (cosmetics, preproduction pellets, tyre wear particles, synthetic fibres, macroplastic degradation) and environmental factors (weathering, biotransformation, currents) to consider. Studies have modelled and estimated plastic inputs into the marine environment and future estimates of plastic concentrations (Jambeck et al., 2015; Lau et al., 2020), with a few estimating future microplastics concentrations (Boucher and Friot, 2017; Everaert et al., 2018, 2020; Isobe et al., 2019). However, these models work on assumptions which can introduce caveats such as not including all sources of plastics/microplastics, not all microplastic sizes considered, plastic considered microplastics one year after release, which data set was used as a baseline, and geographical limitations. Subsequently there is a large variation in predicted microplastic concentrations, yet all models agree that concentrations will be significantly higher, particularly in coastal areas and enclosed seas with large population such as the Mediterranean and South China Sea (Everaert et al., 2020). As there is little consensus among current studies regarding future microplastics concentrations, we used experimental studies that used high microplastic concentration to understand the impact and their frequency on each group of organisms (Fig. 1, Supplementary materials S2.1).

3. Results

3.1. *Ecosystem services of marine zooplankton*

In Table 1, we provide a high-level summary of the different ecosystem services that zooplankton provide. Due to the current limited literature, the examples we highlight are not an exhaustive list, but are considered a good indicator of their provision. This table is divided into the different categories of provisioning, regulating, cultural, and supporting services, which also included definitions and examples of the services provided. Following on from this in Section 3.1.1, we provide an



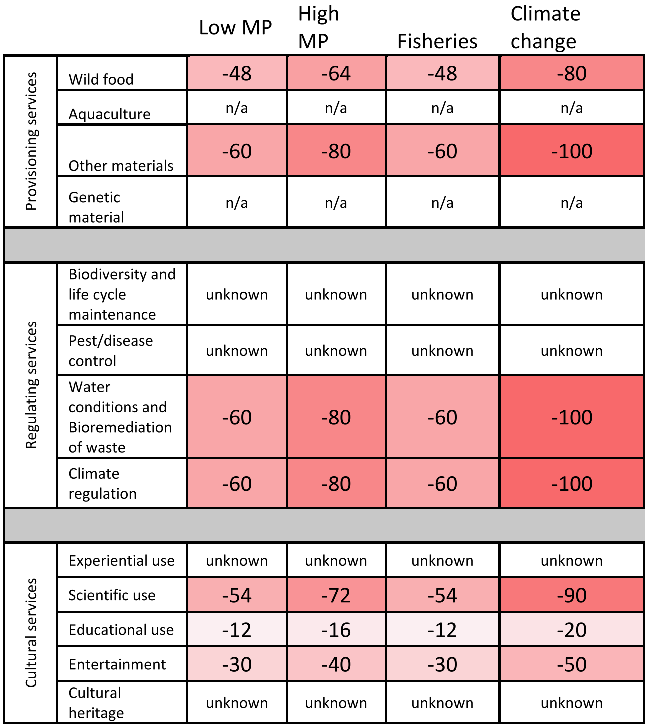
a) Copepods

		Low MP	High MP	Fisheries	Climate change
Provisioning services	Wild food	-12	-18	-4	20
	Aquaculture	n/a	n/a	n/a	n/a
	Other materials	unknown	unknown	unknown	unknown
	Genetic material	n/a	n/a	n/a	n/a
Regulating services	Biodiversity and life cycle maintenance	unknown	unknown	unknown	unknown
	Pest/disease control	unknown	unknown	unknown	unknown
	Water conditions and Bioremediation of waste	-50	-90	-20	-100
	Climate regulation	-50	-90	-20	-100
Cultural services	Experiential use	unknown	unknown	unknown	unknown
	Scientific use	-45	-81	-18	-90
	Educational use	-10	-18	-4	-20
	Entertainment	-60	-90	-20	-100
	Cultural heritage	n/a	n/a	n/a	n/a

b) Jellyfish

		Low MP	High MP	Fisheries	Climate change
Provisioning services	Wild food	-48	-56	-48	80
	Aquaculture	-30	-35	-30	50
	Other materials	-12	-14	-12	20
	Genetic material	-60	-70	-60	100
Regulating services	Biodiversity and life cycle maintenance	12	14	12	-20
	Pest/disease control	-36	-42	-36	60
	Water conditions and Bioremediation of waste	-60	-70	-60	100
	Climate regulation	-60	-70	-60	100
Cultural services	Experiential use	60	70	60	-100
	Scientific use	-54	-63	-54	90
	Educational use	-60	-70	-60	100
	Entertainment	-60	-70	-60	100
	Cultural heritage	-10	-14	-12	20

c) Krill



		Low MP	High MP	Fisheries	Climate change
Provisioning services	Wild food	-48	-64	-48	-80
	Aquaculture	n/a	n/a	n/a	n/a
	Other materials	-60	-80	-60	-100
	Genetic material	n/a	n/a	n/a	n/a
Regulating services	Biodiversity and life cycle maintenance	unknown	unknown	unknown	unknown
	Pest/disease control	unknown	unknown	unknown	unknown
	Water conditions and Bioremediation of waste	-60	-80	-60	-100
	Climate regulation	-60	-80	-60	-100
Cultural services	Experiential use	unknown	unknown	unknown	unknown
	Scientific use	-54	-72	-54	-90
	Educational use	-12	-16	-12	-20
	Entertainment	-30	-40	-30	-50
	Cultural heritage	unknown	unknown	unknown	unknown

Fig. 1. Impacts of the stressors on the ecosystem services of a) copepods, b) jellyfish and c) krill. Scores show the combined exact values of the ecological impact synthesis (Table 3 & 4) and the translation to ecosystem services impacts with a minimum of −100 (in red) indicating the most negative impacts and + 100 (in blue) indicating the most positive impacts. A negative score could indicate either a loss of ecosystem service or a gain in ecosystem disservice. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Overview of the ecosystem services of marine zooplankton.

Ecosystem Service category	Description of category	Evidence for Ecosystem service	Reference
Provisioning services			
Wild food and aquaculture	The use of zooplankton species for human consumption	Shrimp as food source	(Nicol and Foster, 2016)
		Krill used to make krill oil supplements	(Kwantes and Grundmann, 2015)
		Copepods used to make Calanus oil supplements	(Gasmi et al., 2020)
		Jellyfish as food source	(Khong et al., 2016; Brotz and Pauly, 2017; Behera et al., 2020; FAO, 2021)
Other materials	The use of zooplankton species for activities other than consumption	Krill used to make fish meal used for animal feed, aquarium feeds and bait	(FAO, 2021)
		Copepods cultured for live aquaculture and aquaria feed	(Abate et al., 2015)
		Jellyfish used as a soil fertiliser	(Emadodin et al., 2020)
		Collagen extracted from jellyfish used in several biomedical applications	(Addad et al., 2011; Hoyer et al., 2014; Felician et al., 2019)
Genetic material	The use of zooplankton genetic material	Jellyfish genetic material used widely in medical and chemical research e.g., Green Fluorescent Protein (GFP) used extensively in cellular research.	(Zimmer, 2002)
Regulating services			
Climate regulation	Importance of zooplankton in sequestering carbon in the deep sea	Zooplankton play important part in the biological carbon pump by feeding on phytoplankton in surface waters and producing sinking faecal pellets. Carbon is also sequestered through the deposition of dead zooplankton. Copepods also further contribute to carbon sequestration through the lipid pump.	(Phillips et al., 2009; Henschke et al., 2013; Doyle et al., 2014; Jónasdóttir et al., 2015; Belcher et al., 2017; Steinberg and Landry, 2017; Koski et al., 2020; Mayor et al., 2020; Trebilco et al., 2020; Wiedmann et al., 2020)
Pest/disease control	Importance of zooplankton in controlling invasive species populations	Native North Sea jellyfish has been shown to predate on invasive ctenophore	(Hosia and Titelman, 2011; Doyle et al., 2014)
Water conditions and bioremediation of waste	Importance of zooplankton in regulating waste (e.g., nutrients, chemicals)	Jellyfish and copepods can reduce nitrogen & phosphorus concentrations, also a remedial system for coastal environments	(Li et al., 2014; Kumar et al., 2016)
Biodiversity and life cycle maintenance	Importance of zooplankton in regulating biodiversity	Jellyfish at low densities regulate dominant fish populations therefore freeing up resources for other species	(Doyle et al., 2014)
Cultural services			
Cultural heritage	Importance of zooplankton in cultural traditions and folklore	Arrival of box jellyfish as seasonal indicators to aboriginal communities (Woppaburra)	(Authority, 2017)
Scientific use	The direct or indirect use of zooplankton in scientific activities	Jellyfish provided the basis for understanding anaphylaxis. Isolation of the Green Fluorescent Pigment (GFP) from jellyfish which is used extensively in cellular research. Copepods commonly used for ecotoxicology experiments, measuring effects of environmental pollutants.	(Marcus, 2004; Graham et al., 2014; Ensibi et al., 2017; Drira et al., 2018; Botterell et al., 2019)
Educational use	The direct or indirect use of zooplankton in educational activities or materials	Jellyfish exhibited in aquariums	(Graham et al., 2014)
		Medical education regarding jellyfish stings	(Kan *et al.*, 2016; Suriyan *et al.*, 2019)
Entertainment	Interactions where zooplankton are used directly or indirectly for the sole purpose of entertainment	Jellyfish exhibited in aquariums	(Doyle et al., 2014; Graham et al., 2014)
		Zooplankton are popular characters in movies and TV shows	(Ziegelmayer, 2014)
		Jellyfish that lack a notable sting, bioluminescent mixotrophic dinoflagellates and jellyfish are popular tourist attractions	(Cimino et al., 2018)
Experiential use	Direct experience of watching living zooplankton	The well-being benefits (including 'sense of wonder') from interacting with jellyfish	(Jørgensen, 2016)
Supporting services			
Nutrient cycling	Importance of zooplankton in nutrient cycling in oceans	Krill play important role of iron cycling in the Southern Ocean. Zooplankton important for N and P cycling	(Tovar-Sanchez et al., 2007; Alcaraz et al., 2014; Jónasdóttir et al., 2015; Ratnarajah and Bowie, 2016)
Food source for higher trophic levels	Importance of zooplankton as a food source for other species	Zooplankton, particularly copepods and krill, are important food source for many species and play an important role in the distribution of	(Bryant et al., 1981; Henschke et al., 2013; Wei and Zhu, 2017)

(*continued on next page*)

Table 1 (*continued*)

Ecosystem Service category	Description of category	Evidence for Ecosystem service	Reference
		fish, whales, seabirds etc.	
		Sinking dead zooplankton and faecal pellets can provide essential food to the benthos	(Henschke et al., 2013)
Larvae recruitment to fisheries	Importance of zooplankton for larval recruitment to fisheries	Fish and crustaceans have a larval development stage within the zooplankton	(Botterell et al., 2019)
Hosts and refugia for various other animals	Importance of zooplankton as a host or refugia	Jellyfish often harbour juvenile fish and crustaceans under their bells or among their tentacles.	(Gasca et al., 2007, 2015)

in-depth discussion of each of the services provided in each category.

3.1.1. *Provisioning services*

Jellyfish have been traditionally (Table 1) fished in China for over 1700 years (Omori and Nakano, 2001). Whilst China remains the dominant consumer and producer (via mariculture) of jellyfish (60% of global capture production) their popularity has spread over the last 50 years throughout East and Southeast Asia including Japan, Malaysia, South Korea, and Singapore (Pauly et al., 2009). A total of 38 species of jellyfish haven been reported to be consumed globally with the majority of those in the Order Rhizostomeae, which are typically larger and have more rigid bodies which through processing produce a desired crunchy texture (Brotz *et al.* 2016; Behera *et al.* 2020). Jellyfish fisheries typically have a short fishing season of a few months and have large fluctuations in abundance and biomass. There are now emerging fisheries in countries such as USA, Nicaragua, Bahrain and Iran, to combat the negative impacts of jellyfish swarms and provide consumers in Asia with jellyfish out of season (Brotz *et al.* 2016; Behera *et al.* 2020). Whilst catch data is scarce there are now 19 countries fishing for jellyfish with an estimated average annual landing of 900 000 tonnes (Brotz *et al.,* 2016).

Small species of planktonic shrimp (*Acetes* spp) are also consumed in Southeast Asia in the form of shrimp paste which is used in many traditional dishes (Hajeb and Jinap, 2012). Most of the shrimp is caught by local artisanal fishers therefore catch data is limited. However, catch data has been reported for *Acetes japonicus* which reported over 530 000 tones was landed in 2016 (FAO, 2021).

Many products have emerged from the krill fishery with the early focus aimed at human consumption, now the catch is mainly used for aquaculture feed but a growing percentage is used to produce valuable krill oil (Suzuki and Shibata, 1990; Nicol and Foster, 2016). A dietary supplement for omega 3 and substitute for fish oil, it is widely consumed with a growing market due to a rise in health-conscious consumers particularly in developed nations. It has been estimated to be worth USD 275.6 million in 2019 (GVR, 2021). There is also a new further alternative for omega 3 supplements called Calanus oil, extracted from the copepod *Calanus finmarchicus* (Zooca, 2021). Whilst still an emerging fishery, in Norway 10 licenses have now been granted and a total annual quota of 254 000 tonnes can be harvested (Zooca, 2021).

The majority of krill caught are used to make krill meal for use in aquaculture feed and bait (Nicol and Foster, 2016). The high nutrition content of krill including essential amino acids, long chain fatty acids and the pigment astaxanthin have been shown to accelerate growth and enhance palatability through taste and colour of fish and shrimp (Olsen et al., 2006; Castro et al., 2018). Copepods are also used in aquaria feed as either a frozen feed or a live feed (Abate et al., 2020; Zooca, 2021).

Some species of jellyfish contain high levels of collagen, in the last decade this collagen resource has been developed into several applications for use in the biomedical industry including use as collagen scaffolds for tissue engineering and wound/regenerative medicine (Addad et al., 2011; Hoyer et al., 2014; Felician et al., 2019). Jellyfish collagen has a number of advantages over other collagen sources; it is non-mammalian, there is a reduced risk of disease (i.e., BSE), it can be handled at room temperature and it can be sustainably sourced (Flaig et al., 2020).

Another recently proposed use for jellyfish, to help mitigate the negative effect associated with blooms, is to use them as a soil fertiliser (Emadodin et al., 2020). Research has shown that the application of jellyfish fertiliser increased the nitrogen, phosphorus and potassium content of the soil and significantly enhanced the growth and survival of seedlings (Emadodin et al., 2020).

The isolation of the Green Fluorescent Pigment (GFP) from jellyfish genetic material has been used in countless molecular and cell biology experiments as a biological marker of gene expression (Zimmer, 2002).

3.1.2. *Regulating services*

Zooplankton are integral to the biological carbon pump by feeding on phytoplankton in surface waters and producing fast sinking faecal pellets that sequester carbon in the deep sea (Turner, 2002). Copepods and krill are some of the most numerous organisms on the planet and are dominant groups within the zooplankton, they undertake vertical migrations throughout the water column which further aids deposition of faecal pellets, and associated carbon, in deeper water (Bollens and Frost, 1989; Hays et al., 2001; Tarling and Johnson, 2006). Krill are estimated to export 2.3×10^{13} g of carbon each year to the depths from their faecal pellets being released below the mixed layer (Tarling and Johnson, 2006). Diapausing copepods such as *Calanus finmarchicus*, also contribute to carbon sequestration through the vertical transport and metabolism of carbon rich lipids. This seasonal ‘lipid pump’ is highly efficient due to its direct transport to deep water and it has been estimated to double the amount of carbon sequestered by biological process in the North Atlantic (Jónasdóttir et al., 2015). Carbon is also sequestered through the deposition of dead zooplankton with larger species such as salps estimated to export high amounts of carbon to the depths and likely to be a significant carbon input to benthic ecosystems (Henschke et al., 2013; Alcaraz et al., 2014).

Carbon can also be remineralised through grazing on faecal pellets (coprophagy) by zooplankton and microbial degradation (Turner, 2002; Mayor et al., 2020). This process can also aid with bioremediation of waste products such as excess nitrogen and phosphorus in coastal environments with studies showing that both copepods and jellyfish can aid removal of these compounds in the water column (Li et al., 2014; Kumar et al., 2016).

Low level densities of jellyfish can regulate dominant fish populations therefore freeing up resources for other species. In addition, jellyfish have been shown to predate on invasive ctenophores in the North Sea therefore acting as a control on this invasive population (Hosia and Titelman, 2011).

3.1.3. *Cultural services*

Zooplankton contribute to many cultural services including generating tourist revenue, aesthetic and entertainment value, and education. Jellyfish also have important links to cultural heritage and folklore, for example with the arrival of the box jellyfish as a seasonal indicator used by aboriginal communities (Authority, 2017).

Zooplankton can generate tourist revenue through swimming/kayak tours and through public aquaria. Certain species of jellyfish lack a notable sting such as *Mastigias* populations found in Palau which draws over 30,000 visitors annually to swim with them (Graham et al., 2014). Others due to their size i.e., Giant Nomura’s jellyfish (*Nemopilema nomurai*) are popular with recreation SCUBA divers in the Sea of Japan with approximately 1000–15000 people participating in 2009 (Graham et al., 2014). Bioluminescent species found in the zooplankton such as the heterotrophic dinoflagellate *Noctiluca scintillans* (Sea sparkle) and the comb jelly Mnemiopsis leidyi (Sea walnut) generate tourist revenue through night kayak tours in Florida (BKAdventure per comms.). These tours can also provide well-being benefits through experiential use for example generating 'a sense of wonder' (Jørgensen, 2016).

A wide range of species are often on display in aquarium exhibits, but jellyfish are particularly popular especially after Monterey Bay opened their US$3.5 million jellyfish display in 2012 (Graham et al., 2014). These exhibits have been very successful, and they also serve as an important educational activity too. The popularity of marine species, including those found within the zooplankton has spread further in the entertainment industry and are popular characters in films and TV series. All three groups of zooplankton investigated have been the inspiration for characters in popular television series and movies (Plankton from SpongeBob SquarePants, Will and Bill Krill from Happy Feet Two and Ernie & Bernie the Jamaican Jellyfish from Shark Tale) which are now worldwide favourites. They serve as an important educational tool and inspire future generations to be interested in the marine environment.

Zooplankton have been used extensively to further the environmental and medical knowledge base. For example, copepods are commonly used as indicator species in ecotoxicological experiments measuring water quality and/or effects of pollutants such as heavy metals, chemicals and microplastics (Marcus, 2004; Ensibi et al., 2017; Drira et al., 2018; Botterell et al., 2019). Jellyfish genetic material has enabled important discoveries for science including providing the basis for understanding anaphylaxis (1913 Nobel Prize for medicine) and the isolation of the Green Fluorescent Pigment (GFP) (2008 Nobel Prize for chemistry) which is used extensively in cellular research.

3.1.4. *Supporting services*

Zooplankton are an important group of marine organisms at the base of the marine food web. As such they are an important food source for many other species including fish, seabirds, and cetaceans. They also play an important role in the distribution of these species, with many species undertaking extensive migrations to feed on the large abundance of zooplankton which graze on phytoplankton blooms and other zooplankton species (Bryant et al., 1981). Sinking faecal pellets and carcasses also provide essential nutrients to benthic organisms (Henschke et al., 2013).

In addition to carbon, zooplankton play important roles in the cycling of nutrients in the oceans. In the Southern Ocean the micronutrient iron, essential for phytoplankton growth, is limited. Research has shown that much of the iron in the phytoplankton consumed by krill, is released back into the environment via their faecal matter (Ratnarajah and Bowie, 2016; Schmidt et al., 2016). This is then remineralised by bacteria and bioavailable once again to phytoplankton. Though grazing and regeneration of limited nutrients, zooplankton have also been shown to be essential in modifying and maintaining nitrogen and phosphorus ratios in the environment that are available to phytoplankton (Sterner, 1986).

Many species have a pelagic larval stage (meroplankton) within the zooplankton, i.e., fish, oysters, crabs, which when mature are important constituents of fin- and shellfish fisheries. This larval stage allows species, particularly sessile or slow-moving benthic species, to disperse over a wide area and colonise adjacent habitats (Ershova et al., 2019).

In the open ocean there are very few places to hide, however large jellyfish and siphonophores can act as a host and refuge from predators whilst also increasing the food opportunities. Juvenile and small adult fish can hide under their bell or within their tentacles and many species of crustaceans including copepods, barnacles, juvenile crabs are often jellyfish-associated species (Gasca et al., 2007, 2015; Ohtsuka et al., 2009). These buoyant pelagic microhabitats help to sustain oceanic biodiversity (Graham et al., 2014).

3.2. *Ecosystem disservices of marine zooplankton*

Whilst zooplankton provide many important benefits to people (Table 1), many species negatively impact human well-being, including impacts to fisheries, aquaculture, and recreation (Table 2). One of the most notable groups regarding disservices are jellyfish but certain species of copepods also contribute to ecosystem disservices. In Table 2, we provide a high-level summary of the different ecosystem disservices that zooplankton provide, followed by an in-depth discussion of each of the disservices (Section 3.2.1).

3.2.1. *Provisioning disservices*

The same high biological productivity which drives some of the world's largest fisheries also drives jellyfish biomass (Graham et al., 2014). Reported negative impacts of jellyfish blooms on fisheries captures predominantly fall into two categories; decreased quality and quantity of fish, and net management and maintenance (Bosch-Belmar et al., 2020). Globally fishers report clogging and bursting of nets, which not only shortens fishing time but can also increase the risk of capsizing, increased bycatch sorting, and injuries to fishers during sorting and net cleaning (Bosch-Belmar et al., 2020). Blooms can also cause high mortality of fish due to nematocyst stings which can significantly reduce annual catches and lower commercial value. Blooms of *N. nomurai* and *Aurelia* spp. Around Japan and Korea have caused large economic losses to local fishing communities. It has been estimated that the 2005 *N. nomurai* bloom in Japanese waters caused ~ US$300 million of losses (Uye, 2011). Similarly, direct damages to South Korean fisheries due to jellyfish blooms between 2006 and 2010 have been estimated to be between US$68.2–204.6 million per year (Kim et al., 2012). In Peru, a *C. plocamia* bloom in 2008–2009 caused economic loses to the anchovy fishery of over US$200, 000 on only 35 days of fishing, as fishery factories refuse to receive the catch if jellyfish are > 40% of the catch by weight (Quinones et al., 2013). Jellyfish were also reported to have caused over US$10 million in losses to the Gulf of Mexico shrimp fishery in 2001 (Graham et al., 2003).

Aquaculture facilities also suffer from increased mortality and illness in their fish due to jellyfish which can cause complex gill disease (CGD). CGD cause losses of up to 12 % per year in Irish marine farmed salmon (Baxter et al., 2011). Jellyfish nematocyst stings can lead to a local inflammatory response, cell toxicity and disease, with prolonged exposure to the stings often causing secondary bacterial infections, respiratory and osmoregulatory distress behaviour changes and death (Bosch-Belmar et al., 2020). The polyp phase of the jellyfish life cycle, where larvae settle and attach on hard substrates can cause significant biofouling of cages and other submerged aquaculture structures such as piers, ropes, and buoys. This can impact fish farms by causing increases in cleaning costs, restrictions to the water flow through the nets and the seasonal production of stinging medusa adults in close proximity to fish. Another species which causes large losses for fish farms is the sea louse, *Lepeophtheirus salmonis*, an ectoparasitic copepod of salmonid fish. Along with damage to the fins, skin, and gills, which could lead to infection, they have been shown to reduce fish growth and appetite which cause substantial costs to salmon farmers. It has been estimated that the cost of the damages to the Norwegian salmon farming industry due to lice was US$436 million in 2011 (Abolofia et al., 2017). Whilst dependent on location, they also estimate that the total biomass growth lost per production cycle is between 3.62 and 16.55% despite control measures put in place.

Large jellyfish blooms can cause ingression at coastal power plants that use seawater-based condensers and at desalination plants. They can block intake ducts causing temporary shutdown which results in an interruption to energy and freshwater production. Ingression events have been reported globally including Scotland, USA, Israel, Japan and Sweden (Graham et al., 2014). Five jellyfish ingression events at one power station in Malaysia resulted in forced outage and caused ~ US $2.3 million of losses during 2010–2012 (Yee, 2012; (Syazwan et al.,

Table 2

Overview of the ecosystem disservices of marine zooplankton.

Ecosystem disservice category	*Description of category*	*Evidence for Ecosystem disservice*	*Reference*
Provisioning services			
	Negative effect of zooplankton on aquaculture	Jellyfish blooms can cause illness and mortality in fish. Increased cleaning costs due to fouling of submerged structures	(Baxter et al., 2011; Bosch-Belmar et al., 2016, 2020)
Aquaculture		Parasitic copepods (e.g. salmon louse) in large numbers can cause physical damage to fish fins, gills and skins which could lead to infection.	(Costello, 2009; Abolofia et al., 2017)
Fisheries	Negative effect of zooplankton on fisheries	Jellyfish can directly impact fisheries landings, damage to fishing gear, impacts on sizes of commercial fish harvests	(Graham et al., 2003; Uye, 2011; Quinones et al., 2013; Bosch-Belmar et al., 2020)
Fresh water	Negative effect of zooplankton on desalination plants	Jellyfish blooms can cause reduced function of desalination plants by blocking the water intake ducts	(Vaidya, 2005; Daryanabard and Dawson, 2008)
Energy	Negative effect of zooplankton on energy plants	Jellyfish blooms can cause reduced function of energy plants by blocking the water intake ducts	(Yee, 2012; Graham et al., 2014; Syazwan et al., 2020)
Regulating services			
Trophic effects and food web effects	Negative effect of zooplankton on trophic and food webs	Jellyfish blooms can cause trophic cascades, they are a keystone predator at lower trophic levels	(Graham et al., 2014)
Cultural services			
Harmful interactions	Negative effects of zooplankton on human health	Jellyfish (especially box) and Portuguese man o’ war stings can cause pain, paralysis and death	(Fenner, 1999; Fenner and Hadok, 2002; Currie and Jacups, 2005; Graham et al., 2014; Syazwan et al., 2020)
Recreation	Negative effect of zooplankton on recreational activities	Jellyfish blooms lead to reduced tourism at coastal areas	(Kontogianni and Emmanouilides, 2014; Ghermandi et al., 2015; Nunes et al., 2015; Vandendriessche et al., 2016; Vasslides et al., 2018)
Supporting services			
Biodiversity	Negative effect of zooplankton on biodiversity	Increased predation by invasive jellyfish & copepods reduces biodiversity of plankton	(Graham et al., 2003; Goedknegt et al., 2018; Seregin and Popova, 2020)

Table 3

Overview of the Ecological Impact analysis scores for each zooplankton group under each scenario. Extent of impact is defined as the spatial area over which the impact occurs (scored 1–5, 1 = local or regional; 2 = national; 3 = multinational; 4 = continental; 5 = global). Frequency of impact is defined as the percentage of this population (that occurs in the area of impact) that is being impacted (scored 1–5, 1 = very rare (<5%); 2 = rare (6–10%); 3 = occasional (11–15%); 4 = frequent (16–20%); 5 = very frequent (>20%). Direction of impact is defined as either positive (+1) or negative (-1). Magnitude is calculated as (Extent + Frequency) *Direction. See **S2.1 in supplementary** for further in-depth details of scoring.

	Low MP				**High MP**				**Fisheries**				**Climate change**			
	Direction	*Extent*	*Frequency*	*Magnitude =(E + F)*D*	*Direction*	*Extent*	*Frequency*	*Magnitude =(E + F)*D*	*Direction*	*Extent*	*Frequency*	*Magnitude =(E + F)*D*	*Direction*	*Extent*	*Frequency*	*Magnitude =(E + F)*D*
Copepods	−1	5	1	−6	−1	5	4	−9	−1	1	1	−2	−1	5	5	−10
Jellyfish	−1	5	1	−6	−1	5	2	−7	−1	4	2	−6	1	5	5	10
Krill	−1	5	1	−6	−1	5	3	−8	−1	5	1	−6	−1	5	5	−10

2020). Incidences of jellyfish ingression at desalination plants are low due to location of plants in areas of low biological productivity, however in Muscat, Oman the freshwater supply was reduced by 50% for several days in 2003 due to jellyfish blocking the intake ducts (Daryanabard and Dawson, 2008).

3.2.2. Regulating disservices

Jellyfish are a keystone predator at lower trophic levels however when their populations rapidly increase forming blooms or swarms they can cause trophic cascades through suppressing phytoplankton grazers and directly outcompeting zooplanktivorous fish (Schnedler-meyer et al., 2018). This can indirectly affect fisheries through competition predation on fish eggs and larvae and redirected energy flows in food webs (Graham *et al.*2014).

3.2.3. Cultural disservices

One of the most widespread disservices of jellyfish is their ability to sting and injure people which causes concern among beach goers and water sport users. In some rare cases fatalities can occur, the majority of these occur in the tropics, and are due to stings from box jellyfish species. One notable species is *Chironex fleckeri*, which is responsible for over 70 deaths in Northern Australia (Currie and Jacups, 2005; Rachwani, 2021) and has caused hundreds of sting injuries. Smaller species of box jellyfish i.e. *Carukia barnesi* can cause Irukandji syndrome, symptoms include life threating hypertension, cramps in abdomen and limbs, nausea, and pulmonary oedema (Fenner and Hadok, 2002). Unsurprisingly non-stinging jellyfish are often perceived to be harmful, leading to negative perceptions about the beaches and areas in which they have occurred (Graham et al., 2014; Vandendriessche et al., 2016; Syazwan et al., 2020). This can lead to a loss of tourists, a jellyfish outbreak in Israel in 2013 was reported to reduce the number of seaside visits by 3–10.5%, with an estimated annual monetary loss of €1.8–6.2 million (Ghermandi et al., 2015). Of the people surveyed 41% reported that the outbreak had affected the recreational activities they had planned. Another study based also in the Mediterranean, showed that respondents were willing to spend an additional 23.8% in travel time to enjoy a beach with less risk of jellyfish outbreaks (Nunes et al., 2015). There are also direct costs associated with jellyfish stings, aerial medical evacuation in the late 1990′s was estimated to have cost between AU $65,000–1.9 million annually (Fenner, 1999).

3.2.4. Supporting disservices

Invasive species can affect native species and ecosystems directly via competition and predation therefore impacting the local biodiversity. The parasitic copepod *Mytilicola orientalis* was co-introduced with Pacific oysters to Europe and is now found to parasitise native bivalves including blue mussels (Goedknegt et al., 2018). In 2001 a bloom of invasive *Phyllorhiza punctata* jellyfish likely caused millions of dollars of damage to shrimp nets and untold damage via predation on fish eggs and larvae (Graham et al., 2003).

3.3. Ecosystem service impacts due to anthropogenic stressors

This study highlights the many important ecosystem services which zooplankton provide and contribute to human well-being. However, the marine environment is under increasing pressure due to anthropogenic stressors which include microplastic pollution, fisheries, and climate change. These stressors will impact zooplankton and in turn the ecosystem services they provide, and therefore also the accompanying human well-being benefits particularly for coastal communities (Naeem et al., 2016).

3.3.1. Overview of ecological impacts

The ecological impact synthesis evidenced that climate change would have negative impacts on both krill and copepod populations (Table 3). Warming in the Southern Ocean and the resultant reduction of sea ice will have severe negative effects for krill as they are highly dependent on sea ice as it is an important source of food and shelter (David et al., 2021). Similarly, increased temperature and ocean acidification may negatively impact copepod populations through range shifts, and potential effects on growth and reproduction (Garzke et al., 2015; Chivers et al., 2017; Wang et al., 2018; McGinty et al., 2021). On the other hand, warmer temperatures are favourable to most species of jellyfish as this aids reproduction, faster development and expansion of home ranges (Richardson et al., 2009; Treible and Condon, 2019).

Through our ecological impact synthesis, microplastic concentrations are evidenced to have negative impacts on all groups of organisms (Table 3). Current, lower levels of microplastics have a lower frequency of negative impacts but still overlap globally with all groups, with ingestion of microplastics in the field widely shown in copepods and jellyfish species (Desforges et al., 2015; Sun et al., 2017; Iliff et al., 2020). Laboratory studies have shown that high concentrations of microplastics can negatively affect copepod feeding behaviour, growth/development, and reproduction (Lee et al., 2013; Cole et al., 2015; Botterell et al., 2019). Whilst research shows that krill can rapidly egest microplastics with no accumulation (A. Dawson et al., 2018), further research has shown that krill can fragment microplastics into small microplastics and even nanoplastics, which are small enough the translocate through tissue (A. L. Dawson et al., 2018), and can significantly affect swimming behaviour and moulting (Bergami et al., 2020). Already high percentages of jellyfish species are shown to have ingested microplastics, but currently there are limited effects on adult jellyfish. (Sucharitakul et al., 2020) reported no effects of microplastic ingestion on respiration rates or gut epithelium. However, (Costa et al., 2020) reported reduced mobility and pulsation rates in the ephyra life stage, even at the lowest microplastic concentration. Indicating that whilst adults are rarely affected, perhaps larvae stages may be more at risk of microplastic pollution.

Fisheries exist for all the groups investigated, which immediately decreases the population of the zooplankton groups. A fishery for the copepod, *Calanus finmarchicus*, only occurs in the Norwegian Arctic in certain months, the population is closely monitored, and quotas set by government (Marine Resources Act, 2008). Jellyfish are harvested in many countries in Asia and are now expanding to several countries in the Americas and the Middle East (Brotz, 2016). It is difficult to estimate how much of the population is impacted due to the boom/bust nature of swarms and very little population data available (Brotz, 2016). Antarctic krill are the main species of krill that is fished commercially in the Southern Ocean by several countries including China, Republic of Korea, Norway, Chile, Ukraine. Several smaller fisheries also exist in Canada and Japan for Northern Pacific krill (CCAMLR, 2021; FAO, 2021). The krill fishery is managed to ensure that it remains sustainable, with catch limits set each year and modelled on krill abundance with quota data currently set at an estimated 1% available biomass (CCAMLR, 2021).

3.3.2. Impact to ecosystem services

From our ecological impact synthesis of anthropogenic stressors on copepods, krill and jellyfish (Tables 3 & 4, **Supplementary materials S2.1 & 2.2**) and subsequent translation into ecosystem services impacts, we show that the majority of ecosystem services will be negatively impacted with the exception of climate change on jellyfish ecosystem services, which will likely increase. (Fig. 1). Using the positive and negative scores presented in Fig. 1, we discuss below how the ecosystems services of the three groups of organisms may be impacted and the consequences for human well-being.

3.3.3. Impact to provisioning services

Climate change is likely to reduce the range of krill as they are found in polar waters. All stages of the krill life cycle depend on sea ice which is rapidly decreasing due to increasing temperatures (Flores et al., 2012). The reduced amount of ice algae as a food source and the reduced nutrient impacts from melting ice, which helps stimulate large

Table 4

Overview of the ecosystem services scores for each zooplankton group. Extent of impact is defined as the spatial area over which the impact occurs (scored 1–5, 1 = local or regional; 2 = national; 3 = multinational; 4 = continental; 5 = global). Frequency of impact is defined as the percentage of this population (that occurs in the area of impact) that provides this ecosystem service (scored 1–5, 1 = very rare (<5%); 2 = rare (6–10%); 3 = occasional (11–15%); 4 = frequent (16–20%); 5 = very frequent (>20%). Direction of impact is defined as either positive (+1) or negative (-1). Magnitude is calculated as (Extent + Frequency) *Direction. See **S2.2 in supplementary** for further in-depth details of scoring.

		Copepods				**Jellyfish**				**Krill**			
		Direction	*Extent*	*Frequency*	*Magnitude* =*(E + F) *D*	*Direction*	*Extent*	*Frequency*	*Magnitude* =*(E + F) *D*	*Direction*	*Extent*	*Frequency*	*Magnitude* =*(E + F) *D*
Provisioning services	*Food*	1	1	1	2	1	4	4	8	1	5	3	8
	Aquaculture	n/a	n/a	n/a	n/a	1	2	3	5	n/a	n/a	n/a	n/a
	Other materials	unknown	unknown	unknown	unknown	1	1	1	2	1	5	5	10
	Genetic material	n/a	n/a	n/a	n/a	1	5	5	10	n/a	n/a	n/a	n/a
Regulating services	*Biodiversity and life cycle*	unknown	unknown	unknown	unknown	−1	1	1	−2	unknown	unknown	unknown	unknown
	Pest/disease control	0	0	0	0	1	4	2	6	n/a	n/a	n/a	n/a
	Water conditions	1	5	5	10	1	5	5	10	1	5	5	10
	Climate regulation	1	5	5	10	1	5	5	10	1	5	5	10
Cultural services	*Experiential*	n/a	n/a	n/a	n/a	−1	5	5	−10	unknown	unknown	unknown	unknown
	Science	1	5	4	9	1	5	4	9	1	5	4	9
	Education	1	1	1	2	1	5	5	10	1	1	1	2
	Entertainment	1	5	5	10	1	5	5	10	1	3	2	5
	Cultural heritage	n/a	n/a	n/a	n/a	1	1	1	2	unknown	unknown	unknown	unknown

phytoplankton blooms, will have a negative effect on krill populations. Increased temperatures have also shown decreased hatching success and an increase in the percentage of malformed nauplii above 3 °C of warming (Perry et al., 2020).

In copepods, increased temperature and acidification has shown to reduce egg viability and nauplii development (Garzke et al., 2015; Wang et al., 2018). For those species including *C. finmarchicus* that undergo diapause, increased temperatures have shown to decrease the length of diapause, but it is unclear how this will affect the timing with phytoplankton prey availability (Pierson et al., 2013). However recent research using models has shown significant increases in suitable habitat for the subarctic species, *C finmarchicus* at Arctic latitudes (Freer et al., 2022). This range expansion may increase populations available for harvest in fisheries.

These impacts due to climate change may affect the number of both species available for harvesting. Quotas of both species work on harvesting sustainably therefore if overall population numbers change so will the quotas.

High concentrations of microplastics have been shown to have detrimental effects on energy budget, growth/development, and reproduction in copepods (Lee et al., 2013; Cole et al., 2015; Botterell et al., 2019).This will negatively impact copepod populations. Krill have been shown to readily ingest microplastics and fragment them into smaller particles (A. Dawson et al., 2018; A. L. Dawson et al., 2018). The smallest particles, nanoplastics have been shown to negative effect swimming behaviour and moulting in juvenile krill (Bergami et al., 2020). Therefore, microplastics could reduce the number of copepods and krill available to be harvested. The extraction of the oil uses the whole organism (Gigliotti et al., 2011), therefore any ingested microplastics are likely to contaminate the oil. Plastic pollution and microplastics have been highlighted as a contaminant of public concern (Davison et al., 2021). As these are taken as a health food supplement, it raises important questions regarding quality and safety for consumers. Plastic polymers are typically rich in additives (e.g., plasticizers, flame retardants) and can contaminate the flesh of organisms which have potential to put consumers at risk, although this link has not yet been proved (Walkinshaw et al., 2020).

Jellyfish are found to regularly have ingested microplastics (Sun et al., 2018; Iliff *et al.*2020) whilst to date no negative effects have been associated in adults (Sucharitakul *et al.*2020) high concentrations have been shown to negatively affect juveniles (Costa *et al.* 2020). This could negatively affect reproduction and recruitment reducing the number available for harvesting in a fishery that is already seasonal. Whilst only parts of the jellyfish are consumed microplastics are routinely found attached to tentacles which again highlights the risk to human consumption.

Climate change, with warmer sea temperature is likely to benefit jellyfish populations due to faster development and reproduction (Treible and Condon, 2019). Many species will be able to expand their ranges pole wards (Richardson et al., 2009). This will therefore mean more jellyfish available for fisheries and benefit aquaculture facilities. However, this also depends on the willingness of people to eat jellyfish in areas where it is not traditionally consumed (Torri et al., 2020). It also means that there will be more jellyfish genetic material available for use in medical and chemical research.

3.3.4. *Impact to regulating services*

Reduction in the number of copepods could reduce the amount of carbon sequestered and disrupt the biological carbon pump. Additionally, changes to the length of diapause and lipid storage in some copepod species could also affect the amount of carbon sequestered (Jónasdóttir et al., 2015). Research has shown that microplastics can become incorporated into faecal pellets, depending on the type of polymer used this can alter the density of the pellet and therefore alter the speed at which it descends (Cole et al., 2016; Coppock et al., 2019). If faecal pellets descend too slowly, they are consumed by other zooplankton, known as coprophagy, or remineralised by bacteria, therefore never reaching the depths and sequestering carbon.

Jellyfish also sequester significant amount of carbon when they die and sink to the sea floor (jellyfish-falls) (Doyle *et al.* 2014). If their numbers increase due to climate change then they will increase their contributions to the biological pump. All three groups have been shown to regulate and maintain the water conditions through their biological processes (Li *et al.* 2014; Kumar *et al.* 2016). Under the high microplastic concentration scenario the provision of this service will be reduced as evidence shows negative impacts on all three groups. Under the climate change scenario the provision of this service will also be reduced in copepods and krill but will increase in jellyfish as they benefit from warmer waters. Additionally the provision of pest/invasive control by native jellyfish will also be increased under a warmer climate scenario. However increases in jellyfish numbers will negatively impact the services of biodiversity and life cycle maintenance as jellyfish will exert too much predation and remove many larvae and juveniles of other dominant fish species.

3.3.5. *Impact to cultural services*

Whilst for most other services climate change increases the ecosystem services provided by jellyfish, the increase in jellyfish numbers decreases experiential experiences. This is because many people dislike the presence of jellyfish due to injuries through stings or impacts to recreation such as beach closures (Graham et al., 2014). Whilst they are enjoyed in aquaria, they are widely disliked, and increased numbers of jellyfish combined with poleward expansion is likely to further fuel the wariness of them. With the likely rise in jellyfish numbers due in part to climate change, increased education will be imperative to understanding which species are harmful and how to effectively treat a sting injury.

Entertainment and educational services provided by krill or copepods could be reduced with high microplastic concentration and climate change, due to decreased potential to provide inspiration and opportunities. High microplastic concentrations may also decrease those services in jellyfish too.

Services for scientific use will decrease in all groups of organisms under every scenario except for jellyfish and climate change. This is owing to reduction in the populations and therefore less individuals for sampling, for use in experiments, and also for inspiring new scientific questions and ideas.

4. Discussion

In this study, our analysis evidences that zooplankton provide a range of important ecosystem services, including carbon sequestration, food provision, and recreation. We highlight that the anthropogenic stressors of climate change, microplastic pollution, and fisheries predominantly reduce the provision of these ecosystem services, with the exception of climate change on jellyfish ecosystem services which has a mostly positive interaction. High microplastic concentrations and climate change are indicated to have the most substantial negative impacts on both copepods and krill particularly for the ecosystem services of climate regulation, water conditions, other materials, and entertainment. High microplastic concentrations were also shown to have the most negative impact for jellyfish with climate regulation, water conditions, genetic materials, entertainment, and education particularly impacted.

By using low (currently reported) and high (future) microplastic concentration scenarios, it is highly likely that higher microplastic concentration will cause a much larger reduction in ecosystem services provision. It is currently projected that microplastic concentrations are set to increase due to continued inputs into the marine environment and breakdown of macroplastic already present. Therefore, action is required to achieve a reduction in plastic pollution if we are to maintain the sustainable provision of ecosystem services. The implementation of better recycling schemes which include circular recycling, charges for single plastic uses (e.g., UK plastic bag charge) and bans (e.g., UK microbeads in some cosmetics) will all help reduce future plastic inputs into the environment. Continued monitoring of microplastic concentrations found in the field combined with a better understanding of inputs into the marine environment will help to develop more accurate future microplastic concentrations, which is crucial for the development of effective risk assessments. Additionally, dose dependent experiments for every life stage of a species will help to develop endpoints and no-effect thresholds which will be essential to further increase the accuracy and confidence of future ecosystem service impact analyses.

The rise in global temperature and ocean acidification due to climate change is likely to decrease provision of ecosystem services for krill and copepods but likely to increase those of jellyfish. However, increases in jellyfish populations are often associated with blooms or swarms which are also responsible for numerous disservices. In this study we show that there is a clear impact of climate change on zooplankton ecosystem services, and this makes an additional call for action regarding reducing climate change. These kinds of climate change impacts are usually overlooked. By bringing these lesser known, but incredibly important, impacts to the fore, and evidencing them, provides a further argument for the urgency of tackling climate change. Reducing carbon emissions and investing in green energy sources and technology, are essential for limiting the severity of climate change.

Unlike climate change and microplastic pollution, fisheries are not a chronic exposure and each catch immediately decreases the population size. This activity again has a negative impact on all the zooplankton related ecosystem services. It is therefore essential for populations to be monitored and quotas set to ensure that over harvesting does not occur. Currently krill and copepod (*C. finmarchicus*) fisheries are closely monitored with limited number of permits granted each year to ensure the fisheries are sustainably managed (CCAMLR, 2021; Zooca, 2021). However, jellyfish fisheries are not, and typically mimic the bloom bust nature of jellyfish blooms. In some parts of the world this seasonal fishery is a potential solution to the disservices caused by swarms of jellyfish (Brotz et al., 2016).

Within the zooplankton, jellyfish are responsible for the majority of the disservices, which includes their negative global perception due to sting injuries. Increases in jellyfish populations are often associated with blooms or swarms which are responsible for numerous disservices. However, climate change will not necessarily be the sole cause for these rapid increases in jellyfish numbers as there are many other factors that also contribute to blooms which include eutrophication, overfishing, and habitat degradation (Richardson et al., 2009). Copepods can also provide disservices through parasitising salmon reared in aquaculture facilities. These parasitic copepods may benefit from warmer temperatures due to climate change, but the stocking densities of the fish and the conditions in which they are kept will also influence the spread and rise in number of the parasites (Godwin et al., 2021).

Whilst in this study we disaggregated the anthropogenic stressors to understand the extent (regional to global) and frequency of impact occurrence (percentage of population impacted) of each stressor, in reality these stressors will all be occurring simultaneously. Therefore, marine organisms will have to manage with the synergistic effects of multiple stressors. It could be that stand-alone stressors mean species are pushed to the edge of their tolerance threshold, but the combined impact of two or more pushes them beyond it. Recent research has investigated the synergistic effect of ocean acidification and nanoplastic exposure on the early development of krill, reported the lowest success of eggs reaching the limb bud stage in the multi-stressor treatment (Rowlands et al., 2021). Further work investigating the synergistic effects on zooplankton is recommended to further understand the impact on marine ecosystem services. Moreover, there are other stressors on the marine environment, such as oil pollution, eutrophication, and invasive species, that will also influence ecosystem service provision by zooplankton and should also be investigated. To further refine and provide more robust evidence, studies should investigate various stressors and their cumulative effects.

Understanding how these stressors may impact ecosystem services can highlight opportunities and actions. For example, the predicted rise in jellyfish numbers under future climate conditions may open up the possibility of jellyfish consumption in areas where it is not traditionally fished, i.e., Europe and the Americas (Torri et al., 2020). Equally this may lead to the need for increased education and awareness of harmful jellyfish species and the treatment of sting injuries (Kan et al., 2016; Suriyan et al., 2019). Populations of commercially important species should be monitored to ensure that sustainable fisheries are maintained, and jellyfish bycatch should also be included so more accurate catch data can be recorded (Doyle et al., 2014; Brotz, 2016).

A unique aspect of our analysis is that it highlights current knowledge gaps. A number of services in our ecosystem services impact analysis (Fig. 1), scored unknown due to lack of evidence of that ecosystem services provision, whereas not applicable (n/a) indicates that the ecosystem services is not provided. Some services are very specific, for example, 'genetic material' and 'aquaculture', we can therefore have a high level of confidence (see confidence assessment S2.1) that if no evidence is currently present in the literature, the service is currently not applicable as it is not provided. However, some services are much broader, for example 'other materials' and 'biodiversity and life cycle maintenance', where these services could be provided in several different ways and evidence may be concealed within the literature. We therefore have a lower confidence and classify the provision of these services within the impact analysis as currently unknown. Additional information to help inform of further services to fill knowledge gaps could be obtained from the inclusion of grey literature reports. We also highly encourage authors of future research to relate their research, where possible, back to ecosystem services, in terms of which services are provided or which may be impacted. This will aid future ecosystem assessments and provided a wider evidence base which is needed to accurately understand ecosystem service provision and the human wellbeing benefits that they provide.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgements

ZLRB was supported by the Natural Environment Research Council (NERC) through the EnvEast Doctoral Training Partnership (grant number: NE/L002582/1). ZLRB would like to thank Michael Steinke for his supervisory role, and Leanne Hepburn and Claudia Halsband for their helpful comments which improved the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2023.101542.

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