- 1 Progress toward sustainable management of marine crustacean fisheries
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Abstract

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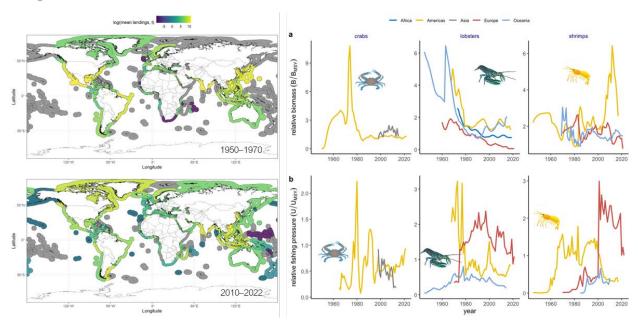
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Marine crustacean capture fisheries have been contributing increasingly more to global aquatic food production in recent decades, helping secure socioeconomic benefits. In the past decade the landings of marine crustaceans rose by more than 67% while expanding spatially and taxonomically, doubling their contribution to global fisheries landings. Although efforts to improve the data collection that informs stock assessments and management decisions have risen to promote sustainability of these fisheries, many stocks remain data-limited and unassessed. For many assessed stocks fishing pressures have declined, but some continue experiencing excessive fishing pressures and remain depleted. Here we review recent progress made to stock assessment methods and management measures applied to both data-limited and -rich crustacean stocks across the globe with particular emphasis on addressing sources of uncertainty. Although an increasing number of assessment methods have been developed to account for various types of uncertainty, evaluation of these methods applied to crustaceans is still limited. Less than onefifth of the recent assessments accounted for multiple types of uncertainty using flexible methods like integrated population models. And uncertainties associated with crustaceans' unique biology were not fully accounted for in estimating key demographic parameters in many assessments. Our review also identifies areas of research to address remaining knowledge gaps, including parameter estimation uncertainties associated with spatial stock structure, incorporating dynamic ecosystem effects, and management implications of accounting for uncertainties. These issues are anticipated to play a greater role in the performance of assessment methods adopted for and thus the management of crustacean fisheries under ongoing environmental change. **Keywords:** stock assessment, integrated model, size-based method, data-limited stock, management strategy evaluation, ecosystem-based management

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Graphic abstract



Global expansion of crustacean fisheries

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The global consumption of aquatic resources has been rising at about double the rate of human population growth in recent decades (FAO 2024b). This demand for aquatic foods is supported increasingly more by marine shellfish fisheries, helping secure socioeconomic benefits in fishing nations (Anderson et al. 2011; Boenish et al. 2022; FAO 2024b). The reported landings of marine crustaceans in particular rose by more than 67% and expanded spatially in the past decade (Fig. 1, Boenish et al. 2022), doubling their contribution to global fisheries landings (8% of total landings, contributing over 23% of total value of seafood production, FAO 2024b). The landings of lobsters (a broadly categorized group in the FAO FishStat database, including *Homarus* spp., Nephrops norvegicus, "rock lobsters", and other crawfishes, FAO 2024a), for example, increased by 80% in the Americas, whereas those of crabs (e.g., *Chionoecetes* spp. and *Callinectes* spp.) and shrimps (e.g., *Penaeus* spp.) increased by 225% and 98% in Asia (Fig. 1, FAO 2024a). The number of commercially exploited crustacean species also rose in many parts of the world; for example, the past decade saw a two-fold increase in crab and shrimp species reported in Europe and a 58% increase in lobster species in Africa (Fig. 2, FAO 2024a). Harvests of these crustaceans provide high economic values, generating up to US\$104 billion annually (23% of an estimated first sale value of US\$452 billion in 2022, FAO 2024b). An increase in demand for and thus economic value of crustaceans can lead to overexploitation when managed poorly (Anderson et al. 2011). Exploitation of a few, high value species can further add ecological pressures to already stressed ecosystems from past human activities (Lotze and Worm 2009). Many crustacean fisheries in Europe and North America, for example, developed and expanded following the depletion of major finfish stocks like Atlantic cod (Gadus morhua) and herring (Clupea harengus) and the stagnation of capture fisheries production

(remaining at ~45% of total aquatic food production) since the 1980s (FAO 2024b; Pauly et al.
1998). The landings of crustaceans such as the American lobster (Homarus americanus) and
northern shrimp (Pandalus borealis) in the northwest Atlantic rose at unprecedented rates
following several big ecosystem and fishery changes (e.g., trophic downgrading, Estes et al.
2011), including the stock collapses of large predatory fishes like cod and climate regime shifts
(Fogarty and Gendron 2004; Mullowney and Baker 2020; Pérez-Rodríguez et al. 2012; Steneck
and Wahle 2013). Some crustacean stocks such as snow crab (Chionoecetes opilio) in the North
Pacific have already experienced stock depletions or collapses in recent years (Mullowney and
Baker 2020; Szuwalski et al. 2023). Because many exploited crustacean species play key
ecological roles in the oceans, depletions of the stocks can ripple through food webs, disrupting
essential ecosystem processes (Boudreau and Worm 2012; Phillips et al. 2013).
Although overexploitation of living marine resources (stock biomass being below a biomass
that produces the maximum sustainable yield, B_{MSY}) remains widespread (Fig. 3, RAM Legacy
Stock Assessment Database 2024), well-managed stocks (through the use of quantitative stock
assessments) can produce more yield and promote sustainable exploitation (Hilborn et al. 2020).
Over three-quarters (76 %) of global fisheries landings in recent years, for example, come from
sustainably managed stocks (FAO 2024b). Collaboration among scientists, managers, and
stakeholders can further help achieve this goal (Goethel et al. 2023b). With growing human
populations, improving the management of crustacean fisheries can better safeguard biodiversity
in the oceans while securing socioeconomic benefits in fisheries-dependent communities and
societies (FAO 2024b).

Managing marine crustacean fisheries for sustainability

Sustainable exploitation of living marine resources stems from science-based evidence that informs management decisions through assessments of stock status and fishing pressure applied (Hilborn and Walters 1992). Exploitation rate, catch rate, and mean body size from a stock assessment are often used as the basis for management decisions to achieve sustainable exploitation of resource populations under varying levels of recruitment (Caddy 2004). Common management measures applied to limit fishing pressure and conserve reproductive potential of the stock include minimum landing size, gear restriction, effort and/or catch control, and seasonal and area closure (Addison and Bennett 1992; Fogarty and Gendron 2004; Siddeek et al. 2004). The data collection to inform management to regulate fishing pressures, however, has lagged behind finfish fisheries in many crustacean fisheries (though there are a few exceptions such as rock lobster (Jasus edwardsii) fisheries in western Australia and snow crab fisheries in the Bering Sea) and these stocks remain data-limited (Perry et al. 1999). Less resource-intensive effort control is thus often adopted when available data or resources are insufficient for stock assessment (Penn et al. 2015). Effort control, however, may become ineffective in regulating catches for species that form seasonal aggregations like spawning events (Armstrong et al. 2013). Technological advancement in gear can also improve fishing efficiency over time, in effect increasing landings under input control (Kleiven et al. 2022). With growing social, economic, and cultural values of shellfish fisheries in recent decades (FAO 2024b), efforts to improve the quality and quantity of data to inform quantitative stock assessments also have risen to promote sustainable exploitation of these fisheries (Phillips and Melville-Smith 2005; Plagányi et al. 2024). Following international agreements like the Code of Conduct for Responsible Fisheries adopted by the Food and Agriculture Organization (FAO) of the United Nations in the late 1990s, the precautionary approach (as opposed to previous reactive

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approaches) to fisheries management began being adopted to minimize the risk of overexploitation of marine living resources despite uncertainty (FAO 1995). Over the past few decades the management of some crustacean fisheries has transitioned from ad hoc systems (Orensanz et al. 1998) to quota-based management systems (through the application of agreed harvest control rules) to improve stock status (size and stability) and economic performance; examples include rock lobster stocks in Australia (Linnane et al. 2023; Penn et al. 2015) and South Africa (Johnston and Butterworth 2005), and crab stocks in Alaska, USA (Heller-Shipley et al. 2021), and crab (e.g., Paralithodes camtschaticus) and shrimp (e.g., Panulirus borealis) stocks in Norway (Hjelset et al. 2024; Hvingel and Zimmermann 2023). In these quota-based management systems, when the reference points (limit and target exploitation rate and stock size) are crossed, a plan that triggers prompt management action (a reduction in catch limit or total allowable catch for example) should be in place to prevent further declines in a stock and rebuild its biomass (Linnane et al. 2023; Penn et al. 2015). Challenges of not meeting management goals and their consequences should be further evaluated by accounting for tradeoffs among multiple (biological, economic, and social) objectives through inclusions of managers' and stakeholders' opinions (Heller-Shipley et al. 2021; Punt and Hobday 2009). Assessing stock status is an essential part of evaluating and applying these decision-based rules (Punt and Hobday 2009; Punt et al. 2012a).

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Assessing crustacean stock status for effective management

A range of assessment methods have been developed to inform fisheries management over the past decades (Hilborn 1992; Hilborn 2003; Perry et al. 1999). Despite high economic values, however, assessment methods for crustaceans have progressed relatively slowly due to a lack of

investment in data collection and stock assessment (Punt 2024). While marine crustacean landings were reported by more than 160 countries in the past decade, crustacean stocks were assessed in less than one-fifth of these countries and comprised less than 30% of all assessed stocks in most of the countries where they were assessed (Fig. 4, Hodgdon et al. 2022; RAM Legacy Stock Assessment Database 2024). In some countries, however, the proportions of assessed crustacean stocks were equal to or higher than those of crustacean landings, such as Spain, Italy, and New Zealand (excluding countries with <5 assessed stocks, Fig. 4). Without effective management informed by quantitative assessments crustacean stocks may follow the familiar scenarios that many finfish stocks had experienced decades earlier, as displayed in Alaskan crab and shrimp fisheries (Orensanz et al. 1998). While fishing pressures on many assessed crustacean stocks have declined in recent decades, some stocks (especially those in Europe) are still depleted (stock biomass being below B_{MSY}) as they continue experiencing excessive fishing pressures (above a fishing mortality rate that produces the maximum sustainable yield, F_{MSY} , Fig. 3). A global review on the stock assessment methods adopted for crustaceans shows high variation among geographical regions and stocks over time (Hodgdon et al. 2022). In general, data

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A global review on the stock assessment methods adopted for crustaceans shows high variation among geographical regions and stocks over time (Hodgdon et al. 2022). In general, data available for many crustacean stocks remains insufficient for traditional analytical stock assessment (Hodgdon et al. 2022; Miethe et al. 2016). Although an increasing number of data-limited assessment methods have been developed in recent decades, evaluation of these methods applied to crustaceans remain limited. Analysts may face further challenges when assessing these stocks because of their unique biology (e.g., lack of permanent calcified structures that record age), preventing them from applying age-based assessment methods often developed to finfish stocks. Some of the assessment methods adopted for these 'hard-to-age' species in the past

include length-based virtual population analysis (VPA), which depends on length-based population structure reconstructed from catch-at-size data and life history information, assuming constant recruitment (Lassen and Medley 2001). Another is length-based cohort analysis, which has been often applied to deterministically compute stock size and exploitation rate, assuming population-in-equilibrium or constant recruitment (Gulland and Rosenberg 1992). In contrast, catch-at-size conditional age methods construct an age-structured model by assigning length classes to age classes, assuming time-invariance in life history processes that influence size-atage like growth (Gulland and Rosenberg 1992). The assumptions made in these methods may, however, be violated for many exploited stocks and result in biased assessments (Punt et al. 2013a; Smith and Addison 2003). The biased assessments can lead to mismanagement if applied (Szuwalski 2022), especially when the stock is managed with size-based measures like minimum landing size (Punt et al. 2013a). Many stock assessment models developed for finfishes also do not capture size-based dynamics of crustaceans well, making these methods less suitable (Punt et al. 2016c). Molting may, for example, bias mortality rate estimates in methods sensitive to life history traits like length-cohort analysis (Bennett 1995). Resulting modeled stock dynamics may produce biased estimates of abundance and size structure, projecting unsustainable yields especially when density-dependent processes like recruitment and variability in habitat condition are ignored (Addison 1986; Caddy 2004). Few methods are, however, developed specifically for crustaceans, with some exceptions like the American lobster in the Gulf of Maine, USA (Chen et al. 2005), snow crab in the Bering Sea (Szuwalski and Turnock 2016), and rock lobster in southern Australian waters (Punt and Kennedy 1997). It remains unclear how well the assessment methods developed for finfish species perform when applied to crustaceans (Hodgdon et al.

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2022; Perry et al. 1999; Punt 2024). In the following we review recent progress made to assessment methods for both data-limited and -rich stocks and their applications to crustaceans by addressing sources of uncertainty (including bias) in the context of the precautionary approach to fisheries management (Caddy 2004) where applicable.

Primary data sources for single-species quantitative stock assessment often comprise catch,

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Applications and challenges of data-limited methods

abundance index, size or age composition, and auxiliary information such as life history traits (Hilborn and Walters 1992). Insufficient data to represent the population or stock is, however, widespread in stock assessments (Maunder and Piner 2015). More than 80% of harvested crustacean stocks are currently broadly categorized as data-limited (Hodgdon et al. 2022); these stocks often lack scientific survey data that characterize their abundance and size or age structure (Carruthers et al. 2014). Of the primary data sources, catch is often the most commonly available type of data on fishing activities (fishery-dependent data) (Pauly and Zeller 2016). An increasing number of catch-based methods have been developed in recent decades to inform management advice through estimation of reference points (Dick and MacCall 2011; Free et al. 2020), including depletioncorrected average catch (MacCall 2009), a depletion-based stock reduction analysis (Dick and MacCall 2011), and catch-MSY (Martell and Froese 2013). These catch-based models are, however, sensitive to assumed depletion levels and can produce biased estimates when stock productivity varies (Carruthers et al. 2014; Pons et al. 2020). When applied to pink spiny lobster (*Palinurus mauritanicus*) in Mauritania, for example, the catch-MSY method produced highly imprecise estimates for stock status (Meissa et al. 2021). But the performance of these methods

can be improved using additional sources of data. When combined with a method fitted to a recruitment index (based on catch surveys of juveniles), for example, an extended depletion model can produce outputs largely comparable to those from more complex models like a lengthbased integrated model, as shown for Australian southern rock lobster stocks (de Lestang and How 2023; Feenstra et al. 2017). Another common type of data available for data-limited stocks (especially in small-scale fisheries in developing nations) is size composition from fishery-dependent sources owing primarily to its low cost and technical expertise required for data collection (Carruthers et al. 2014; Chrysafi and Kuparinen 2016). When estimating management reference points, size composition data in addition to catch data can improve the accuracy and precision of the estimates (Punt et al. 2016c; Rudd et al. 2021) and minimize their sensitivity to recruitment variability. Size frequency data alone can also be used to estimate management-relevant total and fishing mortality rates using methods like the length-based Bayesian biomass (LBB) estimation method (Froese et al. 2018) and the length-based spawning potential ratio (LBSPR) method (Hordyk et al. 2015b), as applied to European lobster (Homarus gammarus) in the North Sea (Miethe et al. 2019). Many size-based methods for data-limited stocks, however, make assumptions about the population and the fishery (steady state, constant average recruitment, etc.) that may not be met in reality (Chrysafi and Kuparinen 2016; Hordyk et al. 2015a; Hordyk et al. 2015b), producing imprecise estimates of stock status and recommended catch limits exceeding sustainable levels (Carruthers et al. 2014; Newman 1995). The LBB method applied to spiny pink lobster in Mauritania, for example, shows model estimates can become unreliable when recruitment is nonstationary and can also produce overly protective optimal landing sizes (Meissa et al. 2021).

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Size composition in catch also may not necessarily represent that of the stock owing to gear selectivity, size-dependent processes, intra- and inter-specific behavioral interactions, and size or sex-based catch limits, likely biasing fishing mortality rate and reference point estimates if not accounted for when using length-based methods (Addison 1986; Bennett 1995; Chrysafi and Kuparinen 2016); this is especially true for short-lived species (Chong et al. 2020; Hordyk et al. 2015b). For crustaceans, spatial and temporal variability in size-dependent parameters such as molting frequency (resulting from ontogenetic shifts in movement) can bias stock status estimates if not accounted for (Bennett 1995). Spatial patterns of fishing operation can further bias size composition in fishery-dependent data when fishers expand fishing areas through localized size-selective depletions of the stock. As such, setting size-based management measures often applied to crustaceans, notably minimum landing size, can be challenging if fecundity-at-size varies and sexual dimorphism is present (Theberge et al. 2024). The efficacy of these management measures or consequences of resulting changes in selectivity thus cannot be addressed using many length-based methods alone (Smith and Addison 2003). Outputs from these size-based methods are often sensitive to uncertainty in life history parameters, fishery selectivity, or exploitation level (Chong et al. 2020; Dowling et al. 2019; Hordyk et al. 2015b). The LBSPR method assumes a logistic form of fishery selectivity and may produce biased estimates especially for species with slow life history when the selectivity curve is dome-shaped (Hordyk et al. 2015b; Hordyk et al. 2015c). Dome-shaped selectivity truncates the right hand side of length frequency data and is confounded with mortality, creating biased estimates, though this is addressed in an updated version of the method (Hommik et al. 2020). Many crustacean fisheries are trap- or pot-based and are thus expected to show dome-shaped gear selectivity because of the difficulty of larger animals entering traps through fixed size

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entrances (Heney et al. 2025). Size-dependent variations in fishing mortality within each age (known as Lee's phenomenon, Lee 1912) can also bias spawning stock ratio in the LBSPR method if not accounted for (Hordyk et al. 2016). Fishing mortality and reference point estimates from size-based methods can, however, be improved by accounting for life history strategy (e.g., slow- vs. fast-growing) with asymptotic size especially when the spatial or temporal coverage of the data is limited (Chrysafi and Kuparinen 2016; Miethe et al. 2019). Fishing mortality and reference point estimated from size composition data can, for example, be improved by integrating asymptotic size estimation and estimating size-dependent natural mortality (Kokkalis et al. 2015). A wide range of empirical assessment methods have been developed and applied to many crustacean stocks with limited data. Catch time series data with effort data, for example, can help characterize fishing behavior (localized stock depletion for example) (Fitzgerald et al. 2018). Although time-varying catchability (catch efficiency) may lead to fluctuations in a fisherydependent abundance index (catch per unit effort or CPUE) independent of actual abundance, this can be improved via index standardization (Bishop 2006; Wilberg et al. 2009). In contrast, fishery-independent data to directly estimate relative abundance such as underwater television (UWTV) survey are widely used for some species such as Norway lobster (Nephrops norvegicus) stocks in the northeast Atlantic (Morello et al. 2007), though variability in fishing efficiency may introduce bias in abundance estimates (Dichmont et al. 2006c). This approach can further be improved by joint use of new monitoring technologies like eDNA and AI tools (e.g., for species identification) (Aguzzi et al. 2022). Other indices like pre-recruit abundance, accounting for density dependency and environmental variability, can be informative when

empirically developing catch forecasts, as demonstrated for data-limited crustacean fisheries like

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western and southern rock lobster in Australia (Caputi et al. 2021; Caputi et al. 2014; McGarvey et al. 2024), European lobster in England (Addison 1995), and the American lobster in the Gulf of Maine (Wahle et al. 2009).

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Variations in life history traits may also act as proxies for stock status (Caddy 2004). Because 289 many fisheries are size-selective and many biological processes are size-dependent, size-based 290 291 indicators such as mean (or median) length and length-at-maturity may be used as part of an empirical assessment of stock status or fishing pattern (Beverton and Holt 1956; Chrysafi and 292 293 Kuparinen 2016; Pauly 1990). For crustaceans that molt less frequently as they grow, for example, changes in molting frequency may indicate changes in fishing pressure as larger adults 294 become scarce (Caddy 1992). Persistent deviations in these indicators can then be quantified 295 generally by cumulative sum (CUSUM) control, or more explicitly stock productivity using 296 productivity susceptibility analysis based on life history information like intrinsic growth rate, as 297 298 demonstrated for crab fisheries in California, USA (Fitzgerald et al. 2018). Changes in these 299 indicators may, however, not necessarily be specific to responses to fishing pressure and need to be interpreted carefully when other factors also vary, as they can inflate uncertainty in stock 300 status (Caddy 2004; Fitzgerald et al. 2019). Declines in mean body size, for example, could 301 302 result from high fishing pressure (removal of large adults), from high recruitment success (entrance of small juveniles and density-regulated growth) (Addison 1997; Caddy 2004), or from 303 304 responses to adverse environmental conditions (Mendo et al. 2016). When management 305 measures to maintain reproductive capacity like prohibiting berried (egg-carrying) females from being landed are applied, size-based indicators like length-at-maturity in landed animals may 306 307 also be biased (Miethe et al. 2016). When applying indicator-based methods, thus, use of

multiple indicators can improve the robustness of the assessment (Caddy 2004; Fitzgerald et al. 2019; Mullowney and Baker 2023).

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With catch data and exploitable biomass indices (commercial or survey CPUEs), aggregate biomass models such as surplus production models (SPMs) can capture stock dynamics (biomass production described as a dome-shaped function of stock size) given the fishing pressures applied and provide management reference points (e.g., maximum sustainable yield) (Froese et al. 2017; Kokkalis et al. 2024). These methods are often applicable to 'data-moderate' stocks lacking size or age composition data (Kokkalis et al. 2024). While earlier forms of aggregate biomass models such as Pella and Tomlinson (1969) and Polacheck et al. (1993) have limited capabilities to account for uncertainties, more recent forms like Stochastic surplus Production Model in Continuous Time (SPiCT, Pedersen and Berg 2017) and Just Another Bayesian Biomass Assessment (JABBA, Winker et al. 2018) can capture stock biomass and fisheries dynamics as unobserved states by accounting for process and observation errors (i.e., a statespace model). SPiCT can also account for irregular survey timings using varying timescales (e.g., annually or quarterly) in input data (Pedersen and Berg 2017). A challenge of these models is that key parameters like intrinsic growth rate (r) and carrying capacity (K) are highly correlated and need to be estimated numerically (using maximum likelihood or Markov chain Monte Carlo methods), which can pose estimation challenges (Kokkalis et al. 2024) and necessitate the use of informative priors. The priors should thus be chosen carefully to avoid model misspecification and estimation bias in management reference points (Kokkalis et al. 2024).

Applications of SPMs to crustacean stocks are still limited but the number of assessed stocks is increasing as more data become available (at least 15 years of the data are needed for reliable model estimation, Kokkalis et al. 2024). SPiCT has been applied to crustaceans like Norway

lobster, northern shrimp, and snow crab in the northeast Atlantic (González Herraiz et al. 2023; ICES 2024a). When applied to the Norway lobster stocks off the Iberian coast, for example, stock assessments using SPiCT were able to capture severe stock depletions indicated by survey indices, whereas other data-limited methods like length-based indicators and LBSPR produced overly optimistic stock status estimates when the assumptions were violated (González Herraiz et al. 2023). Using auxiliary information like life history parameters and fishing selectivity (length-at-age, maturity-at-age, selectivity-at-age, etc.), extended versions of aggregate biomass models like JABBA-select can also capture cohort dynamics (accounting for recruitment variability) without age or size data (Winker et al. 2020). These models may, however, perform poorly for crustaceans like snow crab with poorly-defined selectivity curves (Szuwalski and Punt 2015) or time-varying selectivity (Kokkalis et al. 2024), resulting in biased estimates of stock size, exploitation rate, and management reference points (Kokkalis et al. 2024).

Advancing crustacean stock assessment with integrated methods

Integrated assessment methods can project the population dynamics of harvested species by synthesizing multiple sources of data and accounting for a range of uncertainties in data source and parameter estimation (Maunder and Punt 2013; Punt et al. 2013a). These methods applied to size-structured stocks assume all demographic processes and fisheries are size-dependent but when these assumptions are violated (ontogenetic movement for example), the assessment may be biased (Punt et al. 2017). While integrated methods have been increasingly developed and adopted for hard-to-age species, applications to crustaceans are still limited; for example, only ~16% of crustacean stocks reviewed in Hodgdon et al. (2022) are assessed with these models. Of these stocks, supplemented with additional stocks assessed with integrated models in the past

decade (Table 1), ~60% were assessed with length-structured models, whereas the rest were assessed with age-length- or age-structured models (such as Stock Synthesis) (Fig. 5). Examples of size-structured integrated models applied to crustaceans include rock lobsters in Australian waters (Punt and Kennedy 1997), the American lobster in the Gulf of Maine (Chen et al. 2005), snow crab in the Bering Sea (Szuwalski and Turnock 2016), and northern shrimp in the Gulf of Maine (Cao et al. 2017a) and Alaska (Fu and Quinn 2000) (Table 1). Integrated methods can provide flexibility in model complexity depending on data availability, allowing the performance of assessment models to be evaluated more consistently and facilitate the transition from data-limited to -rich methods when sufficient data are collected (Cope 2024; Rudd et al. 2021; Rudd and Thorson 2018; Zhang and Cadigan 2022). Examples of integrated methods developed for data-limited stocks include the length-based Integrated mixed effects (LIME) models (Rudd and Thorson 2018) and Stock Synthesis-Catch and Length (SS-CL) (Cope 2024; Rudd et al. 2021). These methods can be applied to common data-limited situations with fisheries-dependent (catch and/or length composition) data to estimate management-relevant metrics by accounting for biological reality like time-varying recruitment and fishing mortality (Cope 2024; Rudd et al. 2021; Rudd and Thorson 2018). The integrated methods can perform better (in accuracy and precision) in estimating stock status than other data-limited methods, though the integrated methods may produce imprecise estimates for long-lived species when the temporal coverage of data is limited (Pons et al. 2020; Rudd and Thorson 2018). Despite flexibility there are still unresolved issues associated with the development of integrated models for crustaceans. In the following we review the literature (complemented by the reports on the stocks assessed with integrated population models in the past decade, Table 1) on recent progress made to address model parameter estimation issues (growth,

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reproduction/recruitment, natural mortality, and selectivity) and their possible solutions relevant to crustaceans where applicable.

Growth. Reliable growth rates are critical in assessing stock status and quantifying management reference points in size-structured models (Chang et al. 2012; Punt et al. 2013a). Most crustacean species grow discretely through molting without retaining any hard structure that records age (like fish otolith), posing challenges in estimating growth (Chang et al. 2012; Punt et al. 2013a; Smith and Addison 2003). Some species (e.g., tanner crab Chionoecetes bairdi) even show determinate growth, ending with a terminal molt (Chang et al. 2012; Szuwalski and Turnock 2016), which can pose a challenge in estimation of natural mortality without age information. While several ageing methods have been developed for some crustacean species (Huntsberger et al. 2024; Kilada et al. 2012), obtaining reliable age information remains a challenge when conducting a stock assessment (Chang et al. 2012; Punt et al. 2013a). Bias introduced by incorrectly estimating growth rates can propagate through parametrization of the assessment model (Chang et al. 2012; Punt et al. 2016c). Not accounting for time-varying growth in size-structured models, for example, may produce biased estimates of size structure and in turn selectivity (Cao et al. 2017b).

Many size-structured models use growth models like the von Bertalanffy model to estimate growth deterministically (Sullivan et al. 1990) but research demonstrates that probabilistic approaches using the Schnute model (a more general form of growth model, Schnute 1981) better perform in an assessment model for species with discrete growth (Punt et al. 2016c; Punt et al. 1997). Of the recently assessed crustacean stocks, 60% used the von Bertalanffy model and 19% used the Schnute-Francis model, whereas 21% estimated growth rates empirically using tagging (or other empirical) data to generate size transition matrices (Fig. 5). With size transition

matrices, crustacean growth can be modeled by a two-step process: individuals grow from one (pre-molt) size class to another given the probability of molting (Chang et al. 2012). The twostep approach can also be extended to account for other state variables that influence the molting probability like shell condition (Bradshaw et al. 2025; Punt et al. 2013a). Likewise, maturity can be modeled via size transition and molting probability (Bradshaw et al. 2025; Punt et al. 2013a). For short-lived species (e.g., Pandalid shrimp) shorter time steps (monthly or quarterly) may be needed to account for fast growth (Cao et al. 2017a). Further, variation in growth among individuals can bias growth parameter estimates (Cronin-Fine and Punt 2020; Punt et al. 2009). Size class (or bin) is often pre-defined but can be dynamically modeled (McGarvey et al. 2007), which can be further expanded to account for variability in size-dependent processes within each age such as higher fishing mortality in fast-growing animals in the population (Zhang and Cadigan 2022). Size transition matrices can be estimated either externally or internally in an assessment model using tagging and size frequency data (Millar and Nottingham 2019; Punt et al. 2016c; Siddeek et al. 2016; Zheng et al. 1995). But estimating internally has some advantages when tagging data is incomplete (Siddeek et al. 2016), allowing uncertainty in size-transition parameters to be estimated (Punt et al. 2010), an option also considered best practice (Punt 2024). In contrast, estimating externally may result in growth patterns inconsistent with other sources of data used in an assessment model (Punt et al. 2013a). Uncertainty in a size transition matrix can play a critical role in estimating metrics relevant to management measures in size-structured population models (Punt et al. 2016c; Szuwalski and Punt 2012) and in turn the efficacy of these measures (Chen and Wilson 2002). The mature male biomass estimates of golden king crab (Lithodes aequispinus) in Alaska, for example, were

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biased because of estimation errors in growth increment (Siddeek et al. 2017). When estimating size transition matrices, thus, plausibility of other biological processes with pre-specified parameters should be tested by sensitivity analysis or simulation (Punt et al. 2016c). Reproductive traits (size at maturity, molting and breeding cycles, etc.) can also influence catchability and catch rates (Bennett 1995) and in turn size transition probabilities. Males of some crustaceans like snow and tanner crabs in the Bering Sea, for example, skip molting in years with poor winter habitat conditions (Murphy 2019). The seasonal molting cycle of western Australian rock lobster varies along latitudes, reflecting variability in sea temperature (de Lestang and Melville-Smith 2006). Resulting seasonal variations in size composition and sex ratio data may bias growth estimates and harvestable biomass if not accounted for (Murphy 2019; Steneck and Wilson 2001), which is especially relevant for hermaphroditic species like Pandalid shrimp that go through length-dependent sex change and experience sex-biased fishing pressure (Cao et al. 2017a). Size compositions in fishery-dependent data can be shaped by fishing pattern (Addison 1986); selective fishing behavior, for example, can truncate size structure, biasing estimates of size-dependent parameters (Tu et al. 2018). Standardizing size composition data or use of fishery-independent surveys may help improve the estimates in such a case (Siddeek et al. 2016). Reproduction and recruitment. Like finfish stocks, establishing a stock-recruitment (often defined as 0 year-olds or age groups that recruited to fisheries) relationship is essential in stock assessments based on structured population models, estimation of management reference points, and provision of catch advice (Brooks 2024; Maunder and Thorson 2019). But insufficient data or the absence of a detectable stock-recruitment relationship remain major hurdles in assessing sustainable levels of crustacean stocks (Caputi 1993). Assessment models for some stocks

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assume constant recruitment or spawner-independent recruitment, often based on historically observed values (Caputi et al. 2014; Punt et al. 2013a; Smith and Addison 2003). Of the recently assessed stocks, nearly 80% assumed spawner-independent recruitment, whereas ~20% assumed spawner-dependent recruitment using the Ricker or Beverton-Holt model (Fig. 5). A metaanalysis on more than 200 fish and shellfish stocks also showed stronger support for relationships with environmental drivers than spawner biomass (Szuwalski et al. 2015). In several crustacean stocks in western Australia like rock lobster, brown tiger prawn (Penaeus esculentus), and king prawn (Penaeus latisulcatus), for example, spawner abundance contributes little to recruitment variability when accounting for environmental factors (Caputi et al. 2021). Further, the spawner-independent recruitment approach can be robust to uncertainty in environmentally driven recruitment processes (which are often not well defined) when making short-term stock projections (Brooks 2024). While spawner-independent recruitment is supported by empirical evidence (Caputi et al. 2021), past research instructs us that management reference points strongly depend on a stock recruitment relationship, capturing (compensatory or depensatory) density dependence in recruit mortality (Bannister and Addison 1986; Caputi 1993) especially when the stock is depleted (Caputi et al. 2021). If not accounted for when forecasting stock sizes and catch limits, fluctuations in recruitment strength (including regime shifts) may risk overexploitation of a stock (Caputi et al. 2014; Maunder and Thorson 2019), as shown in the northern shrimp stock in the Gulf of Maine (Richards and Hunter 2021). In size-structured integrated models, recruitment can be modeled based on one or more size classes of juveniles (Punt et al. 2013a) and recruitment estimates are often informed by composition data (Maunder and Thorson 2019). For hard-to-agespecies like crustaceans, however, lack of information about recruitment- and fecundity-at-age

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poses challenges in estimation of time-varying year class strength and characterizing spawnerrecruitment relationships (Caputi 1993; Maunder and Thorson 2019; Punt et al. 2013a). These issues hinder estimation of management reference points for stock status and fishing pressure to achieve sustainable fisheries (Caputi 1993; Fitzgerald et al. 2018; Maunder and Thorson 2019). Misspecification in other assessment model components like growth can also bias recruitment estimates (Maunder and Thorson 2019). In such cases, however, integrated methods can estimate demographic and life history parameters such as growth rates internally using tagging data, removing some of the confounding issues within the data and therefore improving estimates of proportions of recruits to different size classes and recruitment strength (Maunder et al. 2023; Punt et al. 2016c; Punt et al. 2013a) and associated uncertainties, as adopted in some assessments like red king crab (Paralithodes camtschaticus) (Zheng and Siddeek 2013) and golden king crab in Alaska (Siddeek et al. 2022). In addition to the lack of age information, uncertainty in larval and adult dispersal and survival of exploited crustaceans can pose challenges in identifying cohorts in size composition data, the source of recruitment, year class strength, and stock-recruitment relationships (Punt et al. 2013a). For example, for some crustacean species, because of long larval stages (e.g., up to 2 years in Jasus edwardsii), their larval dispersal patterns, settlement locations, and recruitment processes are poorly understood (Richards and Hunter 2021). Incomplete knowledge of early life stage dispersal, including distinguishing local mortality from emigration or local density dependency in sedentary species, can bias stock-recruitment relationships (Caddy 2004; Wahle 2003). Further, intense sex-biased exploitation in some crustacean stocks can also distort sex ratio (Heller-Shipley et al. 2021; Orensanz et al. 1998), misinforming estimation of spawner biomass and in turn stock-recruitment relationships if not accounted for (Zheng et al. 1995). In these

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cases, combined with larval surveys (use of pre-recruit abundance to account for recruitment variability), tagging experiments can help explore spatial connectivity among fishing grounds through adult movement (Bennett 1995) and better inform catch forecasts to regulate fishing pressure, as demonstrated for some crustacean and other shellfish fisheries (Caputi et al. 2021; Caputi et al. 2014). Natural mortality, Natural mortality, defined as non-fishing mortality (including disease, predation, starvation, etc.), is another key demographic parameter in structured population models that influences management-relevant metrics and yet remains challenging to estimate (Cao and Chen 2022; Cronin-Fine and Punt 2022; Maunder et al. 2023). Estimation of natural mortality rate is often confounded with that of other demographic parameters (especially growth rate) and selectivity in size-structured integrated assessment models, posing challenges, especially for crustaceans (Cronin-Fine and Punt 2022; Siddeek et al. 2022; Siddeek et al. 2016; Szuwalski 2022). Incorrectly specified selectivity (Butterworth and Punt 1990) or growth (Cronin-Fine and Punt 2022), for example, can bias natural mortality estimates. Of the recently assessed stocks, only ~2% estimated natural mortality internally, whereas the rest pre-specified values or estimated externally by age/size/stage, sex, and/or area (Fig. 5). Indirect methods to estimate natural mortality outside an assessment model are however limited for hard-to-age species like crustaceans. Natural mortality is often estimated empirically using life history information including maximum age, von Bertalanffy growth parameter (k), and asymptotic length, but uncertainty in these life history parameter estimates is relatively high, as shown for blue crab (Callinectes sapidus) in Chesapeake Bay, USA (Hewitt et al. 2007). These uncertainties can bias natural mortality estimates if not accounted for, leading to unreliable stock status estimates (Maunder et al. 2023).

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When estimating natural morality internally in an assessment model, variability in catchability, growth pattern, and spatial distribution can result in unreliable estimates of both fishing and natural mortality rates (Cao and Chen 2022; Cronin-Fine and Punt 2022; Maunder et al. 2023). Assuming constant natural mortality over time (or size, age, or sex) when it is in fact timevarying can bias stock assessment outputs (Cao and Chen 2022; Cao et al. 2017b; Szuwalski 2022). Natural mortality rates internally estimated for eastern Bering Sea snow crab, for example, were highly variable over time (Murphy et al. 2018) and led to big variations in assessment model estimates (Szuwalski 2022). Likewise, spatial variation in natural mortality due to ecosystem processes such as predator-prey overlap can be substantial (Tengvall et al. 2024), posing a challenge for stock assessment. Because of high predation rates on juveniles (Caddy 2004; Maunder et al. 2023), not accounting for size-dependent natural mortality in sizestructured models can further bias stock size and fishing mortality estimates (Cao and Chen 2022; Cao et al. 2017b). In such cases incorporating auxiliary information like predation rate and habitat condition into estimation of time-varying natural mortality may improve model estimates (Cao and Chen 2022). Because of selective (size- or sex-biased) removals caused by management measures or fishers' preference, natural mortality estimates are likely biased when the assessment model is informed by fishery-dependent data alone (Chen et al. 2005; Punt et al. 2016a). When the data are insufficiently informative to estimate natural mortality, models using a range of natural mortality should be weighted and used to inform management decisions (Cope and Hamel 2022). An example of such an ensemble approach is northern shrimp in Skagerrak and Norwegian Deep, with an assessment model that combines three natural mortality assumptions into a weighted stock estimate (Cardinale et al. 2023). Tagging studies can also provide valuable information in

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estimating natural mortality rate (Siddeek et al. 2022) if potential issues (non-mixing, non-reported tags, tag loss, tag-induced mortality, emigration, or changes in behavior, etc.) are properly accounted for (Maunder et al. 2023; Siddeek et al. 2022). These tagging-related issues may be mitigated by close-kin mark-recapture based on population genetics (like parent-offspring or half sibling relationships) to estimate demographic parameters (Bravington et al. 2016; Maunder et al. 2023), perhaps combined with use of ageing methods when applied to crustaceans.

Selectivity. Selectivity, resulting from the probability of selectivity of a given size class by gear given the probability of availability of that size class, is another key parameter that is often confounded with demographic parameters (including natural mortality and recruitment) and can influence estimation of management-relevant metrics in size-structured assessment models (Butterworth et al. 2014; Maunder et al. 2014; Sampson 2014). Like demographic parameters, misspecification of selectivity can bias assessment model outputs, especially for hard-to-age species, whose growth parameters, for example, can be overestimated when relying on size composition data from fishery-dependent sources (Sampson 2014). Management-relevant metrics like catch limits may, however, be less influenced by uncertainty in selectivity than other sources, as demonstrated for South African rock lobster (Butterworth et al. 2014).

Selectivity form can be shaped by an interaction between the spatial distributions (e.g., size- or stage-dependent patterns) of a target species and fishing (Sampson 2014), which can be modeled with an "areas-as-fleets" approach (assuming homogeneity in selectivity in each spatial strata) in an assessment model (Punt et al. 2014). This interaction can result in dome-shaped (population) selectivity (Sampson 2014) and is likely more common in shellfish stocks than asymptotic selectivity, reflecting their behavior and availability to gear and varying fishing pressures among

areas (Pezzack and Duggan 1995). In trap or pot fisheries, for example, the availability and in turn selectivity of sizes can result from a complex interaction between habitat conditions like current and tide, and the sensory and behavioral responses by target and non-target animals to bait and traps (e.g., an escape gap for juveniles) used by fishers (Pezzack and Duggan 1995). Behavioral responses to and species interactions near traps can also reduce the probability of entry for certain species or sizes, as demonstrated for European lobster (Skerritt et al. 2020), the American lobster (Pezzack and Duggan 1995), spiny lobsters (*Palinurus* spp.) (Tuffley et al. 2021), and Cancer crabs (Cancridae) (Skerritt et al. 2020). Further, because discard survival is often high in pot or trap fisheries, onboard selection (e.g., high-grading of catches) may also affect fishery selectivity. In many crustaceans sexual dimorphism in life history traits and demographic rates are prominent and can influence survey and fishery selectivity (Heney et al. 2025; Tuffley et al. 2021). Sexual dimorphism often emerges from sex-specific molting, growth, maturation, (seasonal and ontogenetic) migration patterns, and fishing mortality (e.g., male-only fisheries, Heller-Shipley et al. 2021; Orensanz et al. 1998). Selectivity can also vary over time because of the movement of target species and fishing operation between areas (Sampson 2014) and gear changes. Sex-specific movement, for example, may lead to sex-biased spatial variability in catchability and size distribution, confounding the estimation of exploitation rates based on changes in size distribution (Chang et al. 2010; MacDiarmid 1991; Steneck and Wilson 2001). Of the recently assessed stocks, 38% used sex-specific selectivity curves and ~26% accounted for time-varying selectivity (Fig. 5). Assuming constant selectivity when in fact it is timevarying, for example, can bias assessment model estimates (Sampson 2014). As with agestructured models (Martell and Stewart 2014), size-structured models in general also perform

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better with time-varying selectivity, producing less biased estimates of stock size and other management-relevant metrics (Cronin-Fine and Punt 2021; Maunder et al. 2014; Punt et al. 2014).

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Emerging issues with research needs

Movement and spatial stock dynamics

Although spatial stock structure is a widely recognized source of uncertainty in crustacean stock assessments, it is rarely explicitly accounted for (Orensanz et al. 1998). Of the recently assessed stocks, more than 60% were assessed without any spatial structure (Fig. 5). Seasonal and spatial variations in size composition and sex ratio, for example, often lead to complex population structure in crustaceans (Bennett 1995). For species with limited adult movement such as spiny lobsters in Tasmania and Victoria, Australia (Punt and Kennedy 1997) and the European lobster (Smith et al. 2001) assessments can be done for different management units separately to account for variations in life history traits. For these species spatial variations in growth and other size-dependent processes may influence the accuracy and precision of stock abundance estimates in each management unit (Punt 2003). But for others the movement of target species and spatial variability of fishing operation may pose a range of challenges in stock assessment and management (Goethel et al. 2023a; Perry et al. 1999; Punt 2019). Adult movement and larval dispersal of exploited species that migrate seasonally, for example, influence source-sink dynamics of a metapopulation (Canales et al. 2016; Orensanz et al. 1998; Steneck and Wilson 2001) or connections between inshore and offshore fisheries (Bennett 1995; Murphy et al. 2018). Not accounting for seasonal and ontogenetic spatial distribution shifts (distinction between nursery and spawning areas for example) may bias demographic parameters confounded with movement (like recruitment or survival rate) in size-structured models (Chen et al. 2005; Murphy et al. 2018).

For crustaceans characterizing spatial stock structure (including subpopulations) may minimize

misinterpretation of size composition data when estimating demographic parameters and fishing

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mortality (Maunder et al. 2016; Punt 2023). Spatial and temporal variability in life history parameters (like size-at-maturity) may emerge from molting frequency and in turn growth shaped by environmental conditions (food availability, sea temperature, shelter availability, etc., (Addison 1986; Bennett 1995; Steneck and Wilson 2001). If life history traits vary among management units and this variability is not accounted for in a stock assessment model, management-relevant quantities can be biased (Punt 2003; Punt 2019; Punt and Hobday 2009). Likewise, spatial shifts in fishing activity (serial depletion driven by market demand for example, Cardinale et al. 2023; Perry et al. 1999), may influence estimation of movement patterns, stock status, and management reference points (Goethel et al. 2023a; McGarvey et al. 2010; Orensanz and Jamieson 1998). Size composition data without information about movement and spatial stock structure may thus be insufficient to identify cohorts and patterns in exploitation (Bennett 1995). In such cases tagging studies can help quantify the movement of adult females and the spatial distribution of larvae and juveniles (and thus recruitment variability) (Bennett 1995). Spatial structure in many stock assessments is often determined by the level of data

(recruitment for example) in spatial strata ("areas-as-fleets" assuming homogeneity in each area)

(Szuwalski and Punt 2015) and adopting methods that account for biological processes

aggregation and thus availability (Goethel et al. 2023a; Punt 2019; Szuwalski and Punt 2015).

Owing partly to data deficiency, spatial structure is not well defined for many crustacean stocks

remains a challenge, especially for species with temporal or ontogenetic habitat expansion (Goethel et al. 2023a). One way to implicitly account for spatial stock structure is through survey indices using the same spatial scale used for data collection (Cadigan et al. 2017, McDonald et al. 2021). When applied to northern shrimp stocks in the Gulf of Maine (Cao et al. 2017c) and the Skagerrak-Norwegian Deep (Cardinale et al. 2023), for example, this approach improves the performance of the stock assessment models. Integrating spatial data into spatially explicit population models may further improve model performance by capturing fine-scale spatiotemporally dynamic processes (e.g., seasonal movement) of stocks and fishing fleets especially in an increasingly dynamic environment (Cao et al. 2020; Olmos et al. 2023). Improved knowledge of spatial stock structure can also help develop area-based management measures like development of reserve areas for spawner protection (Perry et al. 1999).

Ecosystem processes and climate change

Exploited marine species experience a range of dynamic ecosystem processes in the oceans that may modulate their demographic rates (growth, survival, migration, etc.) and catchability over space through time and thus regulate their stock dynamics (Goto 2023; Goto et al. 2022b; Phillips et al. 2013). Some crustacean species have long early life stages and their recruitment strength strongly depends on environmental conditions like sea temperature and pH (Caputi 1993; Caputi et al. 2013). Disregarding environmental effects on spawners, for example, can bias stock—recruitment relationships, estimation of stock status, and likely stock projections, as shown for rock lobster in western Australia (Pearce and Phillips 1988). These ecosystem effects may become intensified especially for shellfish species whose life history processes (like molting for crustaceans) rely on habitat quality as the climate becomes warmer and more variable (Caputi et

al. 2013; Punt et al. 2022). More frequent occurrences of marine heatwayes in the past decades, for example, diminished recruitment success and catches of crustacean stocks including brown tiger prawn, rock lobster, blue swimmer crab (Portunus armatus) in western Australia (Caputi et al. 2021; Caputi et al. 2019; Chandrapavan et al. 2019). Responses to increasingly more variable environmental conditions like sea temperature by exploited species may also deviate from the past under a changing climate, making management measures informed by historically observed patterns less effective (Caputi et al. 2021). This poses further challenges to the management of crustacean species (Szuwalski and Punt 2013). Many exploited crab stocks (including snow crab, red king crab, and tanner crab) in the Bering Sea, for example, show declining trends in stock size and productivity that may be unrelated to fishing pressure but be driven by climate-driven changes in environmental conditions like ice cover and sea temperature (Szuwalski et al. 2021). Similar trends may apply for other species such as northern shrimp, especially for stocks at the southern limit of the species range extent [e.g., the Gulf of Maine, Pershing et al. (2021) and the North Sea, Kjesbu et al. (2022)]. Temperature dependence in crustacean growth may drive the size of harvestable biomass when the fishery is regulated based on minimum landing size: as the climate warms, some species may molt less frequently and mature slower, resulting a stock with fewer legal-sized animals (Caputi et al. 2013; Fedewa et al. 2020). Climate change-induced habitat conditions may also prompt some species to systematically modify their geographical distributions (through adult migration and larval dispersal and survival) to mitigate adverse effects of changing habitat conditions, reshaping local marine community dynamics and fisheries catches (Caputi et al. 2013; Szuwalski et al. 2021). The range shifts of marine species have been increasingly more documented in recent decades (Hollowed et al. 2013; Sorte et al. 2010). But this strategy to mitigate climate

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change-induced stress may be limited for some species, especially in high-latitude systems, where transformation rates in ecosystem structure and process are more accelerated (Henson et al. 2017). Snow crab in the Bering Sea, for example, whose juveniles depend on cold bottom habitat patches as a predation refuge, experienced habitat contraction and shifts in demographic structure (maturity, sex, size, etc.) in recent years (Fedewa et al. 2020), which, combined with record high stock abundances, led to unprecedented food shortage and ultimately a stock collapse (Szuwalski et al. 2023). When climate change-induced spatial and temporal variability in biological parameters is not accounted for in a stock assessment model, the model could be misspecified and yield biased stock size, fishing mortality, and management reference point estimates, resulting in setting unsustainable catch limits (Cao et al. 2017b; Khalsa et al. 2023; Szuwalski and Hollowed 2016). Since environmental conditions are likely to fluctuate more frequently as climate warms, the assumption of time-invariance in vital parameters should be reevaluated (Punt et al. 2022). Recruitment success of the American lobster stock in Nova Scotia, Canada, for example, depends on local climate conditions, modulating landings size (Harding et al. 1983). Accounting for environmental effects and other ecosystem processes in stock assessment and management, however, remains challenging (Szuwalski and Punt 2013). We cannot effectively forecast the consequences of climate change for the management of exploited species without understanding how affected biological processes should be incorporated into a stock assessment model (Punt et al. 2016b). Despite documented empirical evidence, however, few studies have evaluated how ecosystem processes and climate change influence the performance of quantitative stock

assessments and management strategies for crustaceans (but see Punt et al. 2016b; Szuwalski et

al. 2023; Szuwalski and Punt 2013). Model misspecification due to time-varying parameters such

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as growth or natural morality in response to environmental variability can bias assessment outcomes and thus the performance of management measures applied (Punt et al. 2013b). Of the recently assessed stocks, only 14% accounted for time-varying growth, 12% for natural mortality, and 26% for catchability and selectivity (Fig. 5).

One alternative approach to account for time-varying ecosystem processes (regime shift, species interaction, etc.) when forecasting near-term catch limits may be to adopt dynamic reference points as part of harvest strategies (Berger 2019; Bessell-Browne et al. 2022; Haltuch et al. 2009). Methods that account for variable environments can provide reliable management reference points like unfished biomass, depending on species-specific life history traits (Berger 2019; Bessell-Browne et al. 2022; Haltuch et al. 2009). The consequences of non-stationarity in stock productivity may be more pronounced under directional changes driven by climate change (Berger 2019). When mechanisms underlying time-varying productivity are misspecified, however, harvest strategies based on dynamic reference points may also perform poorly and thus should be evaluated through closed loop simulations prior to implementation (Berger 2019; Bessell-Browne et al. 2022).

Applying precaution to crustacean fisheries management

Stock assessments inform decision making based on agreed management strategies such as harvest control (input or output) rules (HCRs), which link stock status and reference points to management action to mitigate overexploitation of a resource population in the context of a precautionary approach (Patterson et al. 2001). The efficacy of control rules can, however, vary because of incomplete knowledge of the biology, fishery, and management of a stock (Fogarty and Gendron 2004; Zhang et al. 2011). In managing crustacean fisheries, uncertainties in

management-relevant metrics and reference points are not always accounted for in evaluation and application of management measures (Addison and Bennett 1992; Fogarty and Gendron 2004; Siddeek et al. 2004). HCRs developed for data-limited stocks, those based on abundance indices (CPUEs), length compositions, and life history invariants, for example, can perform poorly when uncertainties are accounted for (Jardim et al. 2015). High uncertainty in the drivers of recruitment variability in particular remains prevalent in most stock assessments (Maunder and Piner 2015; Maunder and Thorson 2019). Not accounting for non-stationarity in recruitment (owing to climate-induced ecosystem regime shifts for example) when estimating management reference points could also under- or over-estimate the risk of overexploitation (Fogarty and Gendron 2004; Punt et al. 2016a; Zhang et al. 2011) and the performance of HCRs (Szuwalski and Punt 2013). Quantitatively evaluating how robust management measures are against uncertainties before the implementation would minimize the risk of undesirable outcomes (Sethi 2010); this is especially critical for data-limited fisheries, where high uncertainties exist in stock assessments (input data, assumed parameters, model structure, etc.) (Carruthers et al. 2014). Management strategy evaluation (MSE) is one tool for such purpose used in fisheries management, allowing quantification of trade-offs among short- and long-term management (conservation and socioeconomic) goals of stakeholders and promoting transparency in decision-making process (ICES 2019; Punt 2017; Punt et al. 2016a). MSE is designed to evaluate the performance of candidate management measures with key uncertainties accounted for through simulations with feedback between natural resources, fishing patterns, and management systems (ICES 2019; Punt et al. 2016a). Some of the early applications of MSE to crustaceans include rock lobster in New Zealand (Starr et al. 1997) and South Africa (Johnston and Butterworth 2005) and tiger

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prawns (*Penaeus semisulcatus* and *P. esculentus*) in Australia (Dichmont et al. 2006a; Dichmont et al. 2006b; Dichmont et al. 2006c).

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Uncertainties in the fisheries management cycle (data collection and processing, stock assessment, and implementation of control rules) can be generally grouped in several types, including process uncertainty, parameter uncertainty, model uncertainty, estimation uncertainty, and implementation uncertainty (Punt et al. 2016a). Candidate management strategies (management procedures) for South African rock lobster, for example, were developed and evaluated to rebuild this highly valuable (but depleted) stock by accounting for a range of uncertainties, including those in growth and recruitment (process uncertainties), and trade-offs among management objectives set by stakeholders (Johnston and Butterworth 2005). While applications of MSE to crustacean or other shellfish fisheries remain limited compared to finfish fisheries, research shows that the performance of management strategies can vary vastly depending on the source and amount of uncertainty in stock assessment methods (Dichmont et al. 2006a; Dichmont et al. 2006b; Punt and Hobday 2009). For example, not accounting for uncertainties in spatial structure in stock assessment and implementation of catch limits for species with limited adult movement like rock lobster can fail to meet management and conservation objectives (Punt and Hobday 2009). Likewise, uncertainties associated with effort allocation by season, species, and stock area, along with time-varying fishing efficiency and fisher behavior can inflate implementation uncertainty, posing challenges in identifying effective control measures to achieve management goals, as demonstrated through MSEs for mixed prawn fisheries in Australia (Dichmont et al. 2006a; Dichmont et al. 2006b; Dichmont et al. 2006c). Management strategy evaluation can also be an effective tool for evaluating (and revising if needed) current data collection and assessment methods (Carruthers et al. 2014; Dichmont et al.

2006c; Punt et al. 2016a). Evaluating risk associated with trade-offs in investing resources for data collection and stock assessment can inform, for example, the management of small-scale fisheries with relatively low economic value, where input control is often used as a management measure (Blamey et al. 2022; Hordyk et al. 2015c; Plagányi et al. 2023). Applications of MSE show that data-limited assessment methods like LBSPR are sufficiently informative to sustainably manage (or rebuild when overexploited) a stock through an iterative effort-based harvest control rule (Hordyk et al. 2015c). This MSE-aided process could also facilitate the transition to more rigorous assessment and management as more data is collected (Hordyk et al. 2015c). In recent decades an increasing number of methods to set output control measures have been developed and simulation-tested as part of efforts of national governments and regional and intergovernmental organizations to apply a precautionary approach to sustainably manage capture fisheries including for data-limited stocks (Carruthers et al. 2014). The performance of data-limited (catch-, depletion-, and abundance-based) methods, however, highly vary depending on input data type, life history, and fishing pattern (Carruthers et al. 2014; ICES 2024b). These methods are especially sensitive to uncertainty in current stock size and stock depletion and perform poorly when stock dynamics are not accounted for (Carruthers et al. 2014), underscoring the need for further research and development. Persistent overestimation of abundance and underestimation of fishing mortality in perceived population status (retrospective pattern) are prevalent in marine fisheries stock assessment (ICES 2020b; Punt et al. 2020) and likely contribute to stock overexploitation and depletion (Brooks and Legault 2016). In such situations MSE can also be an effective tool to evaluate consequences of biased stock assessments (Hordyk et al. 2019; Szuwalski et al. 2017) and optimize reference points to mitigate the adverse effects of applying catch limits based on biased assessments if

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needed (Goto et al. 2022a). For example, when consequences of not accounting for time-varying biological parameters in the stock assessment of rock lobster in Victoria, Australia are evaluated, non-stationarity in recruitment and catchability can more likely result in biased assessments and management failures than non-stationarity in natural mortality and growth (Punt et al. 2013b). Because of high computational cost, a full MSE (with stock assessment) is not always applied (ICES 2019; Pérez-Rodríguez et al. 2022; Punt et al. 2016a). For example, MSEs without stock assessment fully simulated ('short-cut' MSEs, ICES 2020a) are applied to red king crab in Bristol Bay, USA using a range of scientific uncertainty (stock-recruitment relationship, natural mortality, etc.) levels, demonstrating that accounting for more uncertainty can reduce overexploitation risk but also reduce catch limits substantially (Punt et al. 2012b). Likewise, robustness of model-based HCRs for golden king crab in the eastern Aleutian Islands, USA is also evaluated with a similar approach by accounting for four sources of uncertainty; stock recruitment relationship, parameter estimation, initial stock size, and implementation of catch limit (Siddeek et al. 2020). Short-cut MSEs have been also applied when the complexity of an integrated stock assessment makes a full MSE challenging (e.g., northern shrimp in the Skagerrak and Norwegian Deep, ICES 2023). Short-cut MSEs may, however, overestimate the performance of management strategies and underestimate their associated risks of stock depletion (ICES 2020a; Punt et al. 2016a), though optimization of harvest control rules may mitigate these risks (Fischer et al. 2023).

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Synthesis and moving forward

Although crustacean stocks contribute to substantial socioeconomic benefits and food security globally, many crustacean stocks remain data-limited and unassessed. Lack of quantitative

evidence may also pose challenges in justifying investments of financial and human resources by management agencies in data collection, storage, and analysis (FAO 2024b). Reviewing recent advances in stock assessment methods and management measures has identified various shortcomings that still need to be addressed in achieving sustainable management of marine crustacean fisheries.

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Assessment methods: Given the prevalence of data deficiencies in crustacean fisheries, efforts to improve the performance of data limited methods remain integral. Data-limited (empirical or model-based) methods based on commonly collected data types like catch and size composition (or combined multiple data sources) can quantify stock status and fishing pressure to inform management of data-deficient stocks until sufficient data becomes available. The performance of these methods can be improved by the use of demographic, life history, selectivity pattern, or other auxiliary information (e.g., molting probability) of a stock or its phylogenetically related species (based on a meta-analysis for example) (Prince et al. 2015). While more methods have been developed to accommodate a range of data-limited situations in recent decades, assessment methods applied to crustaceans often account for an insufficient amount of uncertainty, likely underestimating the risk of overexploitation. When applying catch- and especially size-based methods applied to crustaceans, the reliability of model output should be simulation-tested by accounting for uncertainty in the data (Carruthers et al. 2014). Of the recently assessed stocks using structured models, 52% applied sensitivity analysis, but less than 1% applied simulation testing (Fig. 5). Evaluating robustness of an assessment model to assumptions made and uncertainty sources by simulation or sensitivity analysis can improve its reliability and avoid taking unnecessary risks in managing the stock (Chrysafi and Kuparinen 2016).

Accounting for uncertainty and incorporating auxiliary information can be done more efficiently using integrated methods, which provide flexibility in model complexity depending on data availability. Integrated methods also streamline the transition from data-limited to -rich situations (Cope 2024). Still, integrating a variety of data sources and biological information about a stock can pose additional challenges in estimating management-relevant quantities for crustacean stocks. First, lack of age information can still pose many challenges in data collection and assessment model development. In size-structured models growth is characterized using a size transition matrix, in which transition probability is influenced by size- and sex-dependent processes like molting and maturity probabilities as well as reproductive traits like breeding cycle. Although recent research has made some progress in development of size transition matrices (Millar and Nottingham 2019), issues remain, including accounting for individual variability in growth (Cronin-Fine and Punt 2020) and terminal molting (Chang et al. 2012). Further, uncertainty stemming from difficulties in identifying cohorts in size composition data and incomplete knowledge about early life histories can also pose a range of challenges in estimating stock-recruitment relationships and estimation of management reference points; combination of larval surveys and tagging studies can help better understand recruitment dynamics. Second, because some biological parameters like growth are also confounded with other model parameters like natural mortality and selectivity, these parameters should be estimated internally (using auxiliary information and tagging data if available) and propagate their uncertainties in the assessment model (Maunder and Punt 2013). Also, model sensitivity to time invariance in biological parameters if assumed should be tested to mitigate potential bias in stock status estimates.

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Uncertainty in spatial stock structure is one potential source of bias rarely accounted for in estimation of assessment model parameters and management reference points (Goethel et al. 2023a). For most crustaceans spatial variability in life history information and movement of a target species (and resulting fishing pattern) can misinform estimation of demographic rates (Murphy et al. 2018; Punt 2003). Accounting for these spatial variations using approaches like "areas-as-fleets", however, remains challenging for many crustacean stocks that have poorly defined spatial structure. Further development of methods that account for fine-scale spatial stock structure through survey indices (Cadigan et al. 2017; McDonald et al. 2021) and spatially explicit models (Cao et al. 2020; Olmos et al. 2023) may provide promising paths forward and also facilitate development of area-based management measures (Perry et al. 1999). Accounting for dynamic ecosystem processes under climate change: Assessment methods and management measures may need to account for increasingly greater spatial and temporal variability in exploited crustacean stock dynamics (Caputi et al. 2013; Szuwalski et al. 2021) to avoid model misspecification and biased estimates under climate change (Cao et al. 2017b; Khalsa et al. 2023; Szuwalski and Hollowed 2016). Amplified variability in habitat conditions like sea temperature are likely to influence the estimation of stock status and management reference points through changes to demographic parameters (growth, natural mortality, recruitment movement, etc.) under varying levels of fishing pressure. One approach to confront climate change-induced variability in ecosystem processes is development of minimally realistic assessment models such as Models of Intermediate Complexity for Ecosystem assessments (MICE), which can integrate climate effects into demographic parameters, along with other ecosystem processes such as species interactions (Plagányi et al. 2014). Another is to consider non-equilibrium management reference points to account for greater non-stationarity in stock

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productivity (Berger 2019; Bessell-Browne et al. 2022; Haltuch et al. 2009) and evaluate these management measures through closed-loop simulations (Berger 2019; Bessell-Browne et al. 2022).

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A precautionary approach to fisheries management: To mitigate the risk of undesirable outcomes, control measures applied to manage exploited species must be robust to a range of uncertainties in input data, model structure, and parameter estimation (Sethi 2010). Closed-loop simulation tools like MSE can be effective for such a purpose, promoting transparency in evaluating tradeoffs among management objectives against uncertainties in the biology, fishery, and management of a stock (Fogarty and Gendron 2004; Zhang et al. 2011). When applying (data-limited and -rich) assessment methods in the context of precautionary approach to fisheries management, simulation testing such as MSE can account for a range of uncertainty and evaluate the performance of the assessment methods under management scenarios (Prince and Hordyk 2019). Select candidate methods/indicators should be evaluated under those scenarios and probabilities of meeting management objectives quantified to provide a range of values for management measures (Carruthers et al. 2014). Because crustacean fisheries remain data-limited and small-scale in most regions, MSE can also be valuable in evaluating trade-offs in investing resources in data collection and stock assessment (Blamey et al. 2022; Hordyk et al. 2015c; Plagányi et al. 2023), facilitating the transition to more data-demanding assessment and management (Hordyk et al. 2015c).

As we face increasingly more variable environmental conditions in the oceans under climate change, assessment methods and management measures should also be expanded to account for the human (socioeconomic) dimensions of crustacean fisheries; this is especially vital in

developing nations where fishing communities would disproportionately experience the 903 904 consequences of climate change-induced effects on fisheries production (Ding et al. 2017). 905 906 Acknowledgements We thank Matt Garratt (Bangor University) for compiling stock assessment reports reviewed in 907 this paper. Some figures use images from the IAN Symbols, courtesy of the Integration and 908 909 Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). 910 911 References 912 Addison J (1986) Density-dependent mortality and the relationship between size composition 913 and fishing effort in lobster populations. Canadian Journal of Fisheries and Aquatic 914 Sciences 43(11):2360-2367 915 Addison JT (1995) Influence of behavioural interactions on lobster distribution and abundance as 916 917 inferred from pot-caught samples. ICES Marine Science Symposia 199:294-300 Addison JT (1997) Lobster stock assessment: report from a workshop; I. Marine and Freshwater 918 Research 48(8):941-944 919 920 Addison JT, Bennett D (1992) Assessment of minimum landing sizes of the edible crab, Cancer 921 pagurus L., on the east coast of England. Fisheries Research 13(1):67-88 Aguzzi J, Chatzievangelou D, Robinson NJ, Bahamon N, Berry A, Carreras M, Company JB, 922 Costa C, del Rio Fernandez J, Falahzadeh A, Fifas S. (2022) Advancing fishery-923 independent stock assessments for the Norway lobster (Nephrops norvegicus) with new 924 925 monitoring technologies. Frontiers in marine science 9:969071

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Tables

Table 1. Crustacean stocks assessed (in 2015-2024) with age- age-size-, or size-structured population models that are included in this review.

species	location	assessment period	reference
Aristaeomorpha foliacea	Central Mediterranean Sea (GSA 9-11)	2005-2021	1
Aristeus antennatus	Northern Alboran Sea and Alboran Island (GSA 1-2)	2002-2022	1
Aristeus antennatus	Balearic Island (GSA 5)	2002-2022	1
Aristeus antennatus	Northern Spain and Gulf of Lions (GSA 6-7)	2004-2022	1
Chionoecetes bairdi	Eastern Bering Sea	1948-2022	2
Chionoecetes opilio	Eastern Bering Sea	1982-2021	3
Farfantepenaeus aztecus	Gulf of Mexico	1984-2017	4
Farfantepenaeus duroarum	Gulf of Mexico	1984-2017	5
Homarus americanus	Gulf of Maine & Georges Bank	1982-2018	6
Homarus americanus	Southern New England, USA	1984-2018	6
Homarus gammarus	Skagerrak, Kattegat and Öresund (Sweden)	1875-2023	7
Jasus edwardsii	New Zealand CRA 1 statistical areas (901, 902, 903, 904, 939)	1945-2018	8
Jasus edwardsii	New Zealand CRA 2 statistical areas (905, 906, 907, 908)	1979-2021	9
Jasus edwardsii	New Zealand CRA 3 statistical areas (909, 910, 911)	1945-2018	10
Jasus edwardsii	New Zealand CRA 4 statistical areas (912, 913, 914, 915, 934)	1945-2019	11
Jasus edwardsii	New Zealand CRA 5 statistical areas (916, 917, 918, 919, 932, 933)	1945-2020	12
Jasus edwardsii	New Zealand CRA 6 statistical areas (940, 941, 942, 943)	1965-2022	13
Jasus edwardsii	New Zealand CRA 7 and CRA 8 statistical areas (920, 921, 922, 923, 924, 925,926, 927, 928)	1945-2020	14
Jasus edwardsii	Victoria, Australia	1978-2022	15
Jasus edwardsii	West Australian Coast	1975-2023	16
Jasus Ialandii	South Africa (areas 1-8)	1910-2023	17
Litopenaeus setiferus	Gulf of Mexico	1984-2017	18
Metanephrops challengeri	Auckland islands, New Zealand	1991-2024	19
Metanephrops challengeri	Bay of Plenty, New Zealand	1986-2022	20
Metanephrops challengeri	Hawke Bay Wairapa, New Zealand	1986-2022	20
Metanephrops challengeri	Mernoo Bank, New Zealand	1990-2021	21
Nephrops norvegicus	Ligurian and North Tyrrhenian Sea (GSA 9)	1994-2021	1
Nephrops norvegicus	Malta Island and South of Sicily (GSA 15, 16)	2005-2021	22
Nephrops norvegicus	Balearic Island (GSA 5)	2009-2022	1
Nephrops norvegicus	Northern Spain (GSA 6)	2009-2022	1
Pandalus borealis	Gulf of Maine	1984-2023	23
Pandalus borealis	Skagerrak and Norwegian Deep	1970-2023	24
Panulirus argus	Caribbean	1983-2016	25
Paralithodes camtschaticus	Bristol Bay, Alaska	1975-2023	26
Paralithodes camtschaticus	Norton Sound, Alaska	1976-2023	27
Parapenaeus longirostris	Corsica Island and western Mediterranean Sea (GSA 8- 11)	2009-2022	1
Parapenaeus longirostris	Northern Alboran Sea (GSA 1)	2002-2022	1
Parapenaeus longirostris	Western Mediterranean Sea (GSA 5-7)	2008-2022	1
Penaeus esculentus	Northern Australia	1970-2021	28
Penaeus semisulcatus	Northern Australia	1970-2021	28
Portunus armatus	Queensland East Coast, Australia	1988-2019	29
Squilla mantis	Adriatic Sea (GSA 17,18)	2004-2020	30

See Table S1 for full reference information.

Figure legends

- **Fig. 1**. Spatial and temporal patterns in marine crustacean fisheries catches. (a) mean annual catch (t) during 1950–1970 and 2010–2022. Lighter colors indicate higher catches; gray indicates no reported catch. (b) Region-specific trends in fisheries catches of all crustaceans and three major taxonomic groups: lobsters, crabs, and shrimps during 1950–2022 (data source: https://www.fao.org/).
- **Fig. 2**. Spatial and temporal patterns in species diversity in marine crustacean fisheries. (a) mean number of reported species during 1950–1970 and 2010–2022. Lighter colors indicate higher species diversity; gray indicates no reported species. (b) Region-specific trends in species diversity in fisheries catches of all crustaceans and three major taxonomic groups: lobsters, crabs, and shrimps during 1950–2022 (data source: https://www.fao.org/).
- **Fig. 3**. Status of assessed major crustacean stocks (crabs, lobsters, and shrimps) with management reference points estimated (n = 91) by region during 1945–2022 (data source: https://www.ramlegacy.org/; v4.65). (a) relative biomass (B/B_{MSY}) and (b) relative fishing pressure (U/U_{MSY}).
- **Fig. 4**. Spatial patterns in the proportions of (a) crustacean catch in total marine capture fisheries catches during 2010–2022 (https://www.fao.org/) and (b) assessed crustacean stocks in all assessed stocks in the RAM Legacy Stock Assessment Database (https://www.ramlegacy.org/; v4.65) with additional stocks included in Hodgdon et al. (2022).
- **Fig. 5**. Features of the age, age-size, and size-structured stock assessment models used for crustacean stocks in the RAM Legacy Stock Assessment Database (https://www.ramlegacy.org/; v4.65) and additional stocks assessed during 2015–2024 that are included in this review (n = 42, Table 1).

Figures Fig. 1.

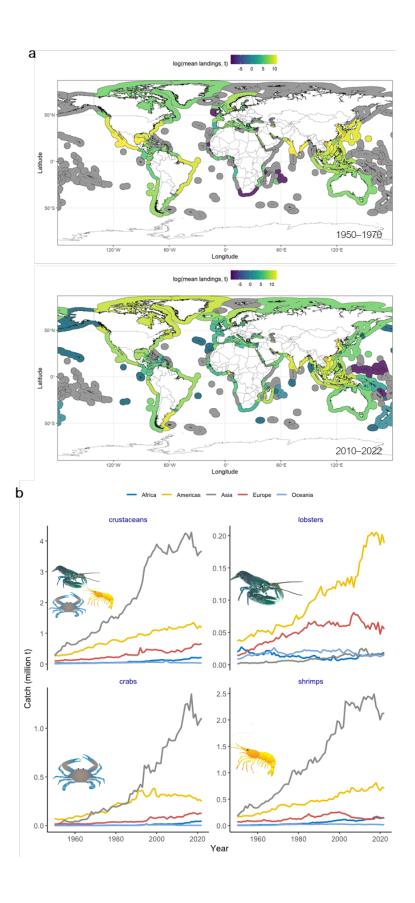
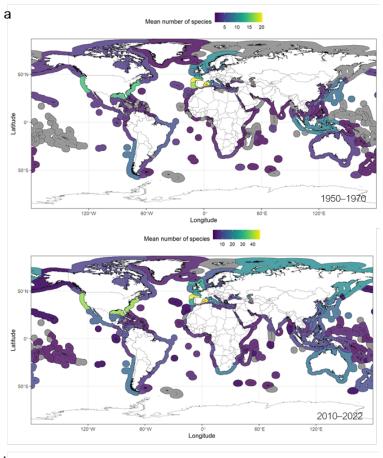


Fig. 2.



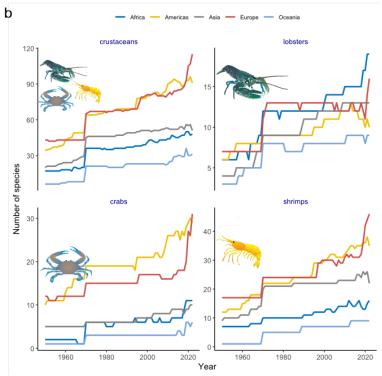


Fig. 3

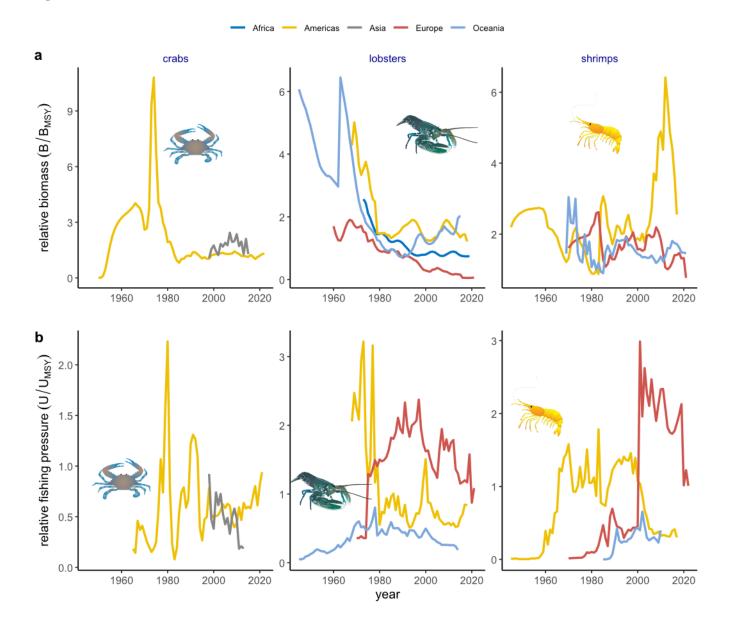


Fig. 4

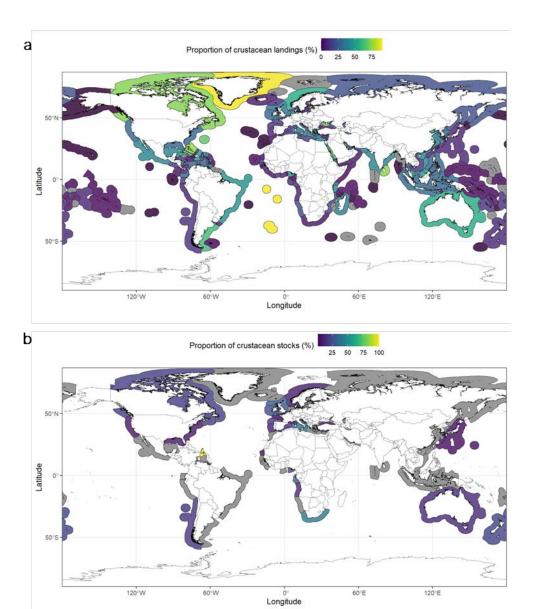
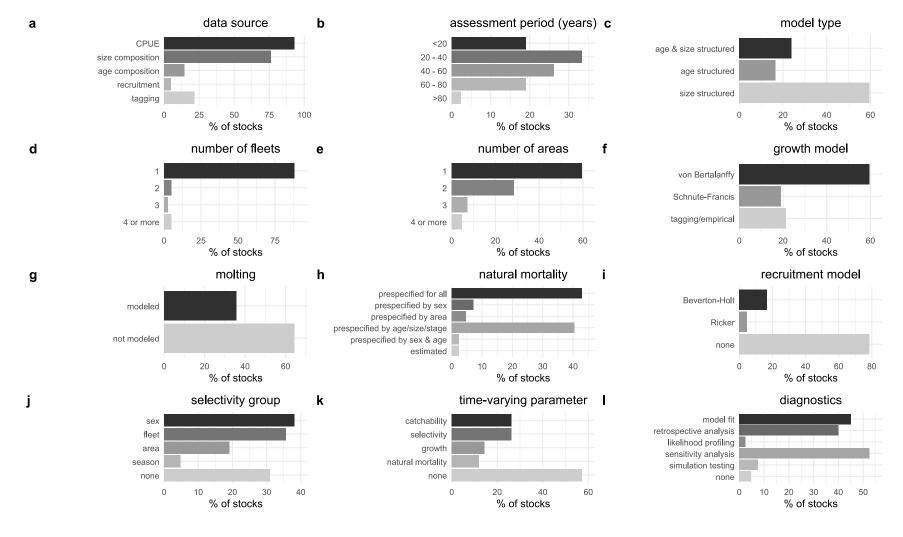


Fig. 5



Supplementary Information

Progress toward sustainable management of marine crustacean fisheries

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Table S1 1. Full reference information for the assessment reports for the crustacean stocks that are included in the review (Table 1).

reference#	reference
1	Scientific, Technical and Economic Committee for Fisheries (STECF). Stock assessments in the
	Western Mediterranean Sea (STECF 23-09), Mannini, A., Ligas, A. and Pierucci, A. editor(s), Publications Office of the European Union, Luxembourg, 2023, doi:10.2760/995295,
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5	Hart, R.A. 2018. Stock assessment update for Pink Shrimp (Farfantepenaeus duorarum) in the
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6	Atlantic states marine fisheries commission. 2020 American lobster benchmark stock assessment
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13	Rudd, M.B.; Webber, D.N.; Starr, P.J.; Roberts, J.O.; Pons, M. 2024. The 2023 stock assessment
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14	Webber, D.N.; Starr, P.J.; Rudd, M.B.; Roberts, J.; Pons, M. 2022. The 2021 stock assessment of
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15	Victorian Fisheries Authority (VFA). 2024. 2022/23 Victorian Rock Lobster Stock Assessment.
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