REVIEWS

Incorporating evolutionary based tools in cephalopod fisheries management

Iva Sabolić · Miguel Baltazar-Soares · Anamaria Štambuk

Abstract With gradual decline of global finfish resources, fisheries targeting cephalopods expanded. Yet, the stock assessment and management practice are frequently lacking, and existing ones often remain poorly suited for cephalopod unique life-history. In light of increasing ecological disturbances in marine ecosystems worldwide, assessing exploited species' status and response becomes vital for devising effective strategies that would ensure their sustainable management. There is generally scarce understanding of the way fisheries and other environmental stressors exert their combined effects on cephalopods stock dynamic and long-term resilience. To that end, evolutionary-based population studies that inform on identity, connectivity and adaptive potential of natural populations present a unique opportunity for assessing the viability of exploited cephalopod stocks. Such studies have been revolutionized in the last decade by proliferation of next generation sequencing technologies. They offer new avenues for expanding our knowledge, especially on population structure and the evolutionary responses to shifts in environmental pressures. In this paper we elaborate on how deep genomic insights into demographic and evolutionary status of fished cephalopods could improve their stock assessment and management practice. We also propose that the common octopus *Octopus vulgaris* would be a suitable model species to test the power of evolutionary tools to inform fishery scientists and managers on biological questions relevant for their sustainable exploitation.

Keywords Stock definition · Sustainable fisheries · Evolutionary potential · Evolutionary genomics · *Octopus vulgaris*

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Status, trends and challenges to global fisheries of cephalopods

Sustainable fishery management is a paradigm whose main goal is to ensure continued biological productivity of exploited stocks (Garcia 2000). Roughly one third of current major world stocks—composed primarily of finfish species—are now considered overfished (FAO 2020). Following the initial increase in global catches after fisheries industrialization in the mid-twentieth century, global fishery exploitation rates peaked in the late 1980s, and remained stable or declined since then (Worm et al. 2009; FAO 2020). However, during the last two decades, substantial efforts and studies have been directed
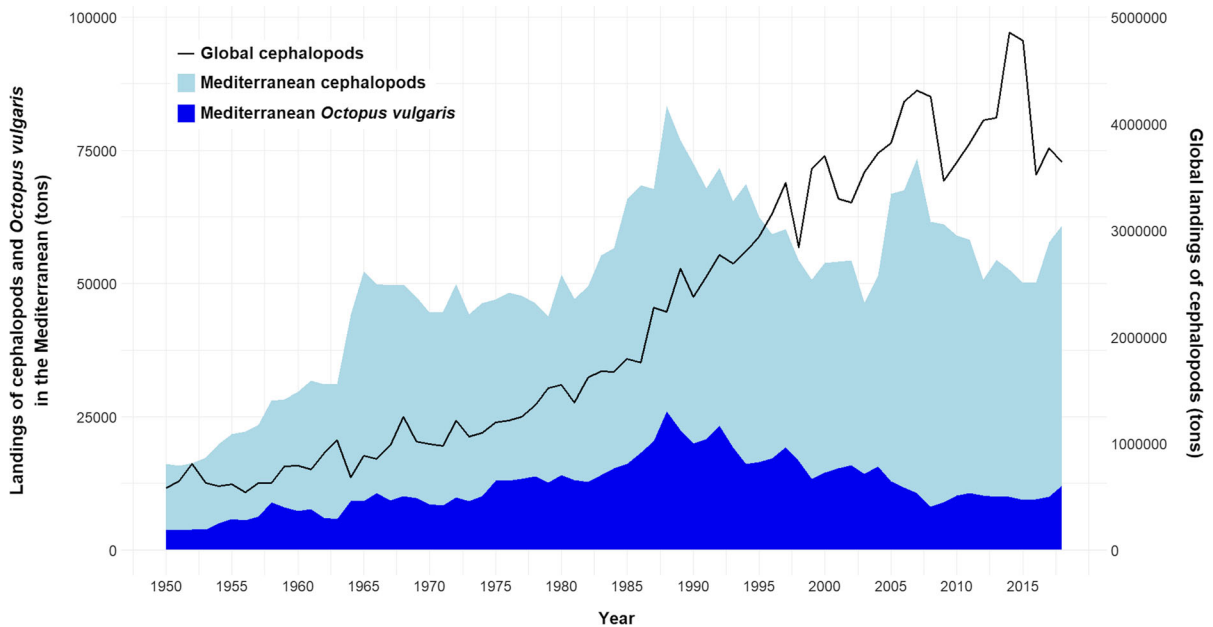
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Fig. 1 Landings of cephalopods and *Octopus vulgaris* from the Mediterranean, and global landings of cephalopods (in tons), covering a time period from 1950 to 2018 (FAO FishstatJ 2020)

towards conservation of the global fishery resources. Improved management legislation and sound policies targeting finfish stocks appear to have succeeded in stabilizing their present-day exploitation in several fishing regions around the world (Worm et al. 2009; Cardinale 2011; Fernandes and Cook 2013). At the same time, the gradual decline in global finfish resources prompted the expansion of invertebrate species fisheries (Anderson et al. 2011).

Traditional small-scale invertebrate fisheries existed around the world for centuries, but in the last decades those have rapidly expanded, and many new fishery areas and practices have emerged (Anderson et al. 2011; Eddy et al. 2017). In the last six years, new record catches have been registered for three invertebrate groups—lobsters, shrimps and cephalopods (FAO 2020). These days, with more than 10 million tons caught annually, and accounting for about 14% of global catches (Eddy et al. 2017; FAO 2020), invertebrate fisheries represent an important socioeconomic component of coastal communities. Furthermore, with the gradual fishing down of food webs, there is an evidence of invertebrate species replacing depleted predator fish at higher trophic levels in marine environment (Molfese et al. 2014; Rogers-Bennett and Juhasz 2014). It is clear that invertebrates

economic and ecological role is becoming ever more relevant for the subsistence of marine ecosystems that are currently on the brink of collapse. If preserved and properly managed, they will have the potential to form the basis of ecosystem services provided by hopefully recovering seas and oceans.

Yet, excluding few highly profitable species, invertebrates fisheries received much less scientific and management attention than most of the exploited vertebrate species so far (Anderson et al. 2011; Eddy et al. 2017). Consequently, for a majority of commercially important invertebrates, accurate data on abundance, population structure and connectivity is lacking, and their stocks are neither effectively assessed nor managed (Anderson et al. 2011; Eddy et al. 2017). Cephalopods are a clear example of invertebrates whose stocks are often inadequately assessed or managed (Arkhipkin et al. 2020), despite their global abundance and landings increasing since 1950s, peaking at 4.9 million tons in 2014, and declining to approx. 3.6 million tons in 2017 and 2018 (FAO 2020, Fig. 1). Over the last years, Food and Agriculture Organization of the United Nations (FAO) has been frequently reporting on the urging situation of the cephalopod fisheries, as simply and clearly stated in their Market report from January 2019

Box 1 Biology, ecology, genetics and fisheries of the common octopus (*Octopus vulgaris*)

The common octopus is a large, muscular, merobenthic cephalopod species that inhabits continental shelf up to 250 m depth (Silva et al. 2002; Norman et al. 2016). They have a fast, non-asymptotic growth rate (Giménez and García 2002) and non-overlapping generations (Smale and Buchan 1981). Spawning occurs all through the year, with seasonal peaks that vary among different geographical regions (Norman et al. 2016; Follesa et al. 2019). The species has high fecundity (Silva et al. 2002), but also experiences high natural mortality rates during juvenile planktonic (paralarvae) and settlement phases of their lifecycle (Boyle and Boletzky 1996). Adults are benthic and confined to limited territories, as most individuals stay within 1 km of foraging radius (Mereu et al. 2015; Arechavala-Lopez et al. 2019). Dispersal is therefore almost exclusively restricted to up to 60 days long planktonic paralarvae stage, which is predominately current-mediated and temperature-dependent (Villanueva 1995). However, recruitment success, development and growth are also strongly determined by environmental factors, primarily the temperature, upwelling (food availability), and rainfall (salinity) (Sobrino et al. 2002; Pierce et al. 2008; Iglesias et al. 2016; García-Martínez et al. 2018), which makes octopus populations prone to sharp fluctuations in spatial and temporal abundance (Boyle and Boletzky 1996). Indeed, environmentally-determined recruitment success has high predictive power of annual octopus landings (Sobrino et al. 2020), and declining trends in octopus landings can sometimes be directly linked to yearly temperature anomalies (Vargas-Yáñez et al. 2009).

Few cryptic species (morphologically similar, but distant species that are treated under the same name) were described within the *O. vulgaris* species complex, and the existence of several more has been proposed (Söller et al. 2000; Leite et al. 2008; Amor et al. 2014, 2017a; De Luca et al. 2014; Lima et al. 2017). Today the distribution of *O. vulgaris* sensu stricto is considered limited to Mediterranean and the adjacent areas of Atlantic Ocean, while other *O. vulgaris*-like populations have been provisionally divided into four *O. vulgaris* types, inhabiting areas of east coast of Central America, southern Brazil, South Africa and eastern Asia (Norman et al. 2016; Amor et al. 2017b). However genetic evidence for such classification is still inconclusive (Van Nieuwenhove et al. 2019), and just recently new species *Octopus americanus* was recognized in the western Atlantic (Avendaño et al. 2020). Several studies reported additional genetic structuring of *O. vulgaris* populations across the Atlantic-Mediterranean border, and between and within Mediterranean basins, where the species status is undisputed (Maltagliati et al. 2002; Cabranes et al. 2008; De Luca et al. 2016). Genetic subgrouping across smaller geographical scales has also been documented, though the oceanographic, ecological, and/or anthropogenic parameters underlying such differentiation remain largely unrecognized (Keskin and Atar 2011; Fadhlaoui-Zid et al. 2012; Melis et al. 2018).

O. vulgaris is considered the most important commercially harvested octopus species (Tsangridis et al. 2002; Norman et al. 2016; Sauer et al. 2019), yet limited management and assessment practices pose a real threat to its overexploitation. Major challenges to their wide-spread management are the octopus' short life cycle, ambiguous species identification, and a population dynamics extremely sensitive to environmental changes (Rodhouse et al. 2014). When looking in the example of Mediterranean, for which a relatively large amount of fishery data is available, the landings of *O. vulgaris* stocks have shown a declining trend since 1980s (Jereb et al. 2015; Quetglas et al. 2015; Sauer et al. 2019; FAO FishstatJ 2020) (Fig. 1). Common octopus fishery is not included in quota regulations under the EU Common Fisheries Policy (Pita et al. 2015b), and laws and regulations governing the management of octopus fisheries in the Mediterranean are generally implemented at regional levels (Arechavala-Lopez et al. 2019). Most countries enforce size limits on caught individuals, along with the restrictions on types and number of gears used, or different seasonal bans (Pierce et al. 2010; Sauer et al. 2019). To the best of our knowledge, only one official assessment of *O. vulgaris* stock was conducted so far in the Mediterranean. It employed stock production model based on the catch per unit effort (CPUE) and landings data from the Balearic Islands area (STECF 2012), and showed that the analyzed stock was unsustainably exploited (STECF 2013).

"*Supplies of both octopus and squid are getting tighter. There is now an urgent need to improve the management of these resources. Overfishing on the high seas and in areas adjacent to national Exclusive Economic Zones (EEZ) is becoming a serious problem. Demand is rising globally, and prices are going through the roof.*" (FAO 2019).

In this review we discuss the benefits of incorporating novel evolutionary genomic tools to inform stock assessment and management of cephalopod fisheries, with special consideration to some of their specific life history traits (Arkhipin et al. 2020) and unresolved complex interactions of environmental and fishery pressures with their population structure and dynamic. We further suggest that the common octopus (*Octopus vulgaris* Cuvier 1797) (Box 1) would be a suitable model for evolutionary-based cephalopod management.

Cephalopods are keystone species and play an important ecological role in many marine ecosystems (Pierce et al. 2008; Gasalla et al. 2010; Eddy et al. 2017; de la Chesnais et al. 2019). Recently, a global increase in the cephalopod abundance has been reported, suggesting that their populations proliferated

in the environments where their main competitors, finfish, have been severely depleted (Doubleday et al. 2016). However, other studies implied that the over-exploitation of cephalopod stocks may already be underway in several regions (Anderson et al. 2011; Rodhouse et al. 2014; Meissa and Gascuel 2015; Sauer et al. 2019). Maintaining the cephalopods fisheries at sustainable levels particularly grows in importance in the light of their high trophic positions, implying that their population collapse might have the ecosystem-wide consequences (Arkhipkin et al. 2020).

Patagonian longfin squid (*Doryteuthis gahi*) and Argentine shortfin squid (*Illex argentinus*) in the Falkland Islands area are among some of the prominent examples of regulated cephalopod fisheries (Payne et al. 2006; Arkhipkin et al. 2015). Their stock management relies on pre-recruit surveys and in-season depletion-based assessments to meet targeted spawning stock biomass (Agnew et al. 2005; Arkhipkin et al. 2020). However, this approach demands the use of special equipment for preseason assessments, and extensive daily data collection during season to appraise and forecast stock population dynamics (Rodhouse et al. 2014; Arkhipkin et al. 2020). For many other cephalopod stocks assessments are conducted within the scope of traditional age-based or stock-recruitment models, which rely on the estimates of spawning stock biomass, size-at-maturation, and fishing mortality. Those estimates are used for predictions of recruitment-mortality relationships, which present one of the primary information sources in implementation of sustainable fishing pressure in finfish (Bourlat et al. 2013; Bernatchez et al. 2017).

Still, such point estimates are not only unsuited for cephalopods unique life histories (Arkhipkin et al. 2020), but possess few drawbacks that drive them a bit away from the biological reality. First, their spatial framework is still largely based on the predefined geo-political boundaries, and not realistic population distributions. Second, they are mainly based on simple life history traits and demographic parameters, often considered as static over generations and extrapolated from one to other stocks of the same species (King and McFarlane 2003; Laugen et al. 2014). This simplified view of stocks as demographic units ignores the ability of populations to adapt in response to the environmental pressures, as well as the possibility of anthropogenic pressure affecting contemporary evolutionary trajectories of populations, or even species (Reid et al. 2016; Ryu et al. 2018).

Improving stock-level knowledge with evolutionary genetics

Exploring the evolutionary potential of exploited stocks

In order to avoid detrimental effects when challenged by the environmental alterations, populations may recourse to three (mutually not exclusive) strategies. They may respond with adjusting their phenotypes (acclimation through phenotypic plasticity), or may migrate to change their distribution. Lastly, they can respond positively to the shifts in selective pressures at the level of populations genomic background, i.e. adapt. In fact, such adaptive biological responses do exist in natural populations and may drive diverse consequences on the level of stock dynamics (Laugen et al. 2014; Kuparinen et al. 2017).

Evolutionary potential can be defined as the capacity of natural populations to undergo such microevolutionary adaptive changes (Eizaguirre and Baltazar-Soares 2014). The net outcome of individual responses to a given pressures dictates the viability of the population in the course of generations (Lande 1988) (Box 2). On the top of the random mortality inherent to early life stages of most marine species, extrinsic pressures directionally select those who survive and reproduce. This invokes further consideration that population abundance and composition are not only regulated by random mortality, but also by selective mortality, which affects the genomic makeup of future generations, and consequently their adaptive potential (Conover et al. 2006). Hence, this microevolutionary perspective should be more comprehensively incorporated into viewpoint of stocks being solely passively ecologically driven (Conover and Munch 2002).

Moreover, such evolutionary standpoint also considers stocks to be connected through the exchange of migrants (gene flow) at different degrees, which may further mediate the processes of local adaptation and/or population restoration in multifaceted ways (e.g. Kawecki and Ebert 2004; Bay et al. 2017). Connectivity also helps restoring fishery induced declines in genetic diversity (Pinsky and Palumbi 2014).

Box 2 Interplay between environmental stressors, and genomic and phenotypic responses shapes contemporary stocks characteristics

Marine organisms are exposed to various environmental stressors, which often act in the combined, synergistic way, and evoke different biological responses at the level of exposed populations (Fig. 2). *Increased mortality*, as a direct consequence of fishing activities, or disease for instance, can quickly result in *population decline*. In a less dramatic way, stressors impact can cause phenotypic and/or genomic change in a population. For example, when mortality occurs in non-random fashion, *selection* acts on certain phenotypes. Changes in *phenotypic characteristics* are well documented among exploited populations, and many studies have linked overfishing and climate change to migrations, earlier age and size at maturation, or decrease of fecundity in fishes (Allendorf and Hard 2009; Kendall et al. 2009; Peer and Miller 2014; Heino et al. 2015; Uusi-Heikkiläa et al. 2017; Yamamoto et al. 2018). Substantial changes in population size or connectivity to other populations, as well as selection toward adapted (or sometimes in the case of anthropogenically induced selection, maladapted) phenotypes, result in *genomic changes*, i.e. shifts in *genetic diversity* and *differentiation*. Those are subtler, but not less pervasive signatures of population alterations. The ability to adapt to upcoming environmental change positively correlates with the genetic diversity within populations—*evolutionary potential*. A decrease in population's genetic diversity can therefore lead towards further population decline by reducing both the individual fitness and evolutionary potential of the whole population (Allendorf et al. 2008). This is particularly common for populations that are genetically isolated or well adapted to specific environments, as they tend to be less diverse within themselves (Lawton et al. 2011). Limited connectivity or genetic specialization through the local adaptation make such populations particularly endangered by changes in external stressors, and constrain their recovery potential. Alternatively, populations that are well connected to others have a constant exchange of juveniles and migrants that ensures the infusion of new genetic material into the population (Lawton et al. 2011). *Connectivity* to other populations may sometimes hamper local adaptive processes, but in its positive context it enables spreading of adaptive variants and increases genetic diversity within populations, and thus plays a crucial role in maintaining the populations stable in face of today's rapidly changing environment.

Resolving connectivity among marine stocks is thus vital for assessing the overall evolutionary potential of the species, and is in addition crucial for effective design of marine protected areas (Palumbi 2003).

Understanding the evolutionary potential of fished stocks is correspondingly becoming critical for assessing their resilience to current and future external pressures (Valenzuela-Quiñonez 2016). Evolutionary potential can be appraised by a multitude of approaches, but perhaps the most often used one is to quantify and qualify the population genetic diversity (Frankham 1996). This approach holds in the assumption of positive correlation between genetic diversity and population viability: populations with high genetic diversity are expected to have higher evolutionary potential (Frankham 1996; Fraser and Bernatchez 2001).

The use of genetic tools is not new in fisheries sciences, and over the decades a variety of genetic markers (e.g. allozymes, microsatellites and mitochondrial DNA) have been used to analyze population structure of commercially exploited marine species (Ward 2000; Silva et al. 2019a). Those studies laid the ground for important mapping of various fished stocks (Hauser and Carvalho 2008; Ovenden et al. 2015). However, recent advances in the development of mass parallel sequencing technologies, hence forth called next generation sequencing (NGS) are revolutionizing the amount of information extracted from the genetic data (Mardis 2008). By producing thousands of genomic markers, it is now possible to make inferences on demographic and evolutionary status and processes at the genome-wide level, which are further corroborated by a more robust statistical support of the analytical framework. Assessing a stock genomic background expands information multi-fold: it can help resolve taxonomic conflicts within species complexes, it provides information on the identity of particular stocks and connectivity among them, informs on the effective population size, allows estimation of genetic diversity—an indicator of population health, and permits the investigation of genetic variants under selection (Frankham 1996; Wang et al. 2016; Bernatchez et al. 2017; Valenzuela-Quiñonez 2016; Silva et al. 2019a, b). All these population characteristics, absent in the traditional stock assessment toolbox, augment our perception of the ways in which environmental alterations, especially anthropogenically-induced ones, can affect the stock dynamics.

Successful implementation of sustainable fisheries governance depends on reliable information on stock identity and status (Hutchinson 2008). Failing to recognize multi-species or multi-population composition of fished stocks can have long reaching consequences and drive fishery collapse of undetected stock
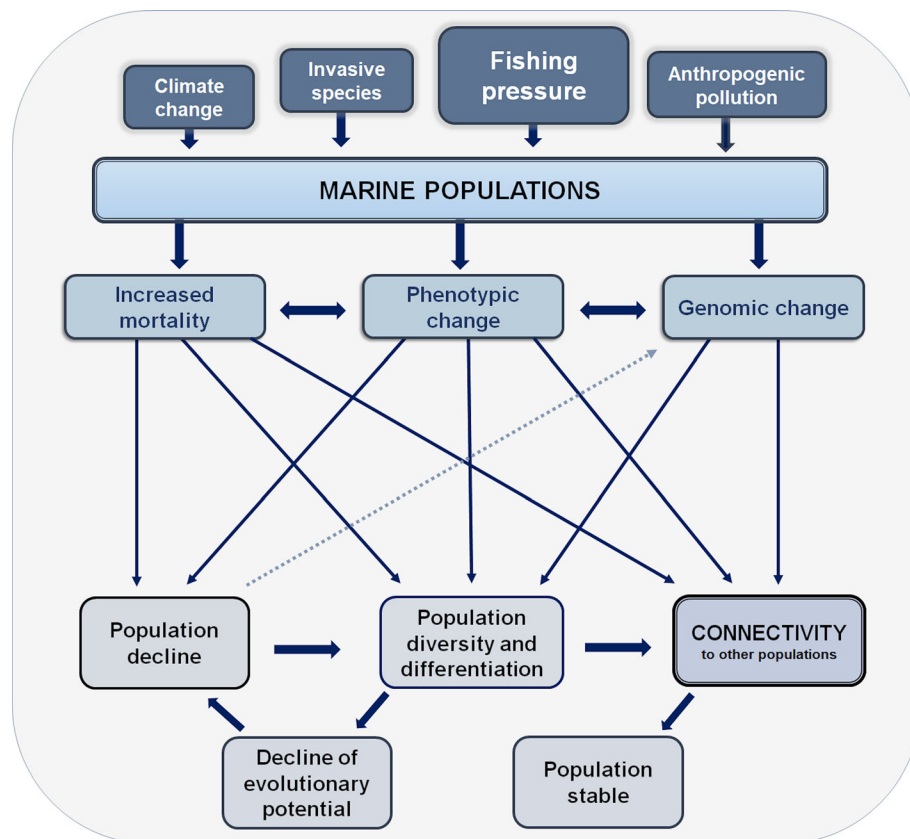
Fig. 2 Interplay between environmental stressors, and genomic and phenotypic responses shapes contemporary stocks characteristics

components (Momigliano et al. 2018 and references therein). From a genetic perspective, the issue of inferring the differentiation and connectivity of marine stocks has always been linked to a lack of resolution provided by commonly used genetic methodologies (Waples and Gaggiotti 2006). This is largely because the absence of firm barriers in marine environment, combined with the planktonic juvenile or highly migratory adult life stages, results in the vast number of migrants in many marine species. When such biology is coupled with low number of traditional genetic markers used to assess population structure, the statistical likelihood to capture genetic variants that could serve as stock-specific diagnostic markers sharply decreases. The mass production of genomic markers via NGS appeared to fill in this information gap (Nielsen et al. 2009), providing high resolution detection of both weak neutral population structure and the adaptive divergence in various commercially important marine species (Valenzuela-Quiñonez

2016). Evolutionary genomics additionally propelled the understanding of stocks migration patterns, and allows individuals assignment even in mixed migrating lineages (Meek et al. 2016; Momigliano et al. 2017).

Exiting new studies are further accumulating on environmentally-driven contemporary evolutionary processes (Lescak et al. 2015; Benestan et al. 2016; Baltazar-Soares et al. 2018; Lehnert et al. 2019). There is increasing evidence that genomic adaptation occurs in marine populations even in the face of the high gene flow (Sanford and Kelly 2011; Tigano and Friesen 2016), and that selection readily acts even on a single generation (Pujolar et al. 2014). Some prominent examples with very clear management implications include revealing of cryptic speciation in Australian mullet (*Mugil cephalus*) and Baltic populations of European flounders (*Platichthys flesus*), or existence of distinct ecotypes in Atlantic and Mediterranean stocks of anchovy (*Engraulis encrasicolus*) (Krück

et al. 2013; Catanese et al. 2017; Momigliano et al. 2017). Moreover, unlike traditional genetics, genomics enables direct link to particular environmental factors underlying population dynamics and structuring. Certain environmental characteristics, such as temperature or salinity, have been found correlating with genomic variants and driving adaptive divergence in the European hake (*Merluccius merluccius*), Atlantic herring (*Clupea harengus*), and Atlantic cod (*Gadus morhua*) (Limborg et al. 2012; Milano et al. 2014; Wenne et al. 2020). Similar seascape genomic studies revealed an adaptive population differentiation related to environmental variables in invertebrates with long lived pelagic larvae: American lobster *Homarus americanus*, greenlip abalone *Haliotis laevigata,* oyster *Crassostrea virginica*, and tabletop corals *Acropora hyacinthus* (Bay and Palumbi 2014; Benestan et al. 2016; Sandoval-Castillo et al. 2018; Bernatchez et al. 2019).

This ongoing environment-evolution interplay is especially gaining on its importance in the wake of today's rapid global environmental change (Halpern et al. 2015) (Fig. 2). Estimating the adaptive potential of marine stocks therefore becomes crucial nowadays as marine populations are increasingly exposed to variety of human induced selective stressors, e.g. ocean acidification that impacts development of early stages (Frommel et al. 2012), overfishing that drives fisheries-induced evolution towards earlier maturation (Heino et al. 2015), pollution that hampers individual fitness and reproduction (Islam and Tanaka 2004), or global warming that affects population dynamics and distribution (Free et al. 2019). In that context, traditional fisheries management practice that perceives stocks as static, geopolitically defined entities is becoming increasingly challenged to incorporate the perspective of fishery stocks as evolutionary units.

Why is the evolutionary toolbox needed in cephalopod fisheries?

Decrease in competition and predation from overfished finfish species, coupled with short generation time and plastic life history characteristics of cephalopods, appear to be at least partly responsible for the global increase in their abundance (Doubleday et al. 2016). In general, cephalopods have long been considered resilient ecological opportunists, quick to recover from exploitation or oscillations in natural conditions. While some authors argue that short lived invertebrate species are rather sensitive to environmental alterations but resistant to overfishing (Kompas and Chu 2018), cephalopods might be an exception to the rule due to their high trophic levels (Meissa and Gascuel 2015). Observed large spatial and temporal fluctuations in cephalopod catches could thus actually be masking local collapses of some species caused by overfishing (Rodhouse et al. 2014). Indeed, in species with discrete generations, overfishing exerts immediate effects on the recruitment of the following generation (Pierce and Guerra 1994).

When mortality increases due to fishing pressure, populations evolutionary response includes shift toward earlier size at maturation to rapidly enhance population growth (Dunlop et al. 2015). The faster the life history, the smaller window remains open for such an adaptive response. Indeed, models show that in species with fast life histories population genetic background is less affected, but such evolutionary constrains also increase the possibility of fishery-induced population collapse at high harvesting rates (Nusslé et al. 2016). Substantial decrease of size at maturation was already observed for fished populations of giant squid (*Dosidicus gigas*) upon El Niño event in the Gulf of California (Hoving et al. 2013), which persisted for subsequent generations. Authors hypothesize the main role of phenotypic plasticity, and this phenomenon is usually mentioned in a context of being the main, if not only, contemporary adaptive process in cephalopods in some other studies (e.g. Repolho et al. 2014; but see van der Vyver et al. 2016). Nevertheless, phenotypic plasticity does not preclude genomic evolution—in nature those processes often go hand by hand, and in terms of affecting the evolutionary trajectories they interact in multiple ways (Pfennig et al. 2010). The important role of environmental selection in shaping the cephalopod genomic and phenotypic variability at larger evolutionary scale cannot be disputed (Lindgren et al. 2012; Ritschard et al. 2019). Heritability estimate of a trait provides information on the relative contribution of direct environmental vs. genetic effects to the phenotypic variance, and is usually used to distinguish between plastic and genetically adaptive responses. Yet, to the best of our knowledge, such studies on cephalopod main life history traits haven't been made to this point, aside from the study reporting on significant heritability of antipredatory behavior in dumpling squid,

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Euprymna tasmanica (Sinn et al. 2006). The relative contribution of phenotypic plasticity and genetic adaptation underlying morphological divergence of cephalopod populations, along with its implications for fishery management, have been previously discussed—for example in the case study of Chokka squid *Loligo reynaudii* (van der Vyver et al. 2016) or Patagonian longfin squid *D. gahi* (McKeown et al. 2019). However, the role of local adaptation in cephalopods has still not been widely investigated. Morse et al. (2018) recently observed distinct signatures of adaptive genomic differentiation in the Australian holobenthic blue ring octopuses *Hapalochlaena maculosa*, and Strugnell et al. (2017) reported environment as important driver of genetic population structuring of the Antarctic octopod species.

While it has been hypothesized that elevated sea temperatures helped drive the observed global increase in cephalopod abundance (Doubleday et al. 2016), populations models also suggest that a rise in sea temperature could quickly turn initial exponential growth of octopus populations into a sharp decline (André et al. 2010). Experimental research further suggests that temperature rise mimicking predicted ocean warming accelerates embryonic development, but decreases survival of octopus early life stages (Repolho et al. 2014).

More importantly, population genetic variation generally does not recover from a decrease as quickly as the population size (Sonsthagen et al. 2017), and such loss can affect the fitness and evolutionary potential of the population in the long-term (Spielman et al. 2004). It is also essential to note that synergistic determinantal impact of overfishing combined with environmental stressors, such as ocean warming, is not anymore just some hypothetical worst-case scenario. The scientific evidence started to build up on such multifaceted ecological interactions (Hamilton et al. 2000; Harley et al. 2006; Pershing et al. 2015; Free et al. 2019). Modeling of fishery and environmental data on 150 commercially exploited populations revealed that combination of overfishing, fast growth and environmental variation substantially increases the probability of population collapse, which, notably, becomes even more likely in the case of delayed management responses (Pinsky and Byler 2015). The link between fast life history and the strength of the global warming impact on fished stocks has also been recently confirmed by Free et al. (2019). And last, but not the least, global change exerts its fishery relevant effect due to declining ecosystem diversity, decreased resilience of exploited stocks, and temperature dependent distribution shifts (Perry et al. 2005; McClenachan et al. 2019). Such distribution shifts have been already documented for cephalopod species, including the octopuses (Ramos et al. 2018).

The understanding of population connectivity patterns is considered a prerequisite for sustainable management of exploited species (McKeown et al. 2019). Again, the applicability of evolutionary genomic approach to resolve such question in cephalopods is starting to become evident. A recent genome-wide study, for instance, helped identify a clinal species pattern among the already mentioned blue ringed octopus populations along the coast of Australia, with gene flow observed among the neighboring populations (Morse et al. 2018).

Overall, there is an obvious lack of understanding of the interferences of fisheries and environmental alterations onto the cephalopod population dynamic. Simultaneously, assessment methods and regulation practices remain maladapted for their unique life-history traits. The current situation hence calls for implementation of novel tools in evaluating the status of exploited cephalopod stocks. In that regard, genomic studies are uniquely suited to provide us with necessary in-depth knowledge on the wild populations, which is crucial for sustaining the viability of exploited stocks. In fact, the scientific framework proposed here has a great potential to fill in already identified knowledge gaps, and to aid addressing three out of the six major challenges cephalopod research is facing nowadays, namely: assessing cephalopod adaptation to environmental alterations, intensifying genetic research, and to design novel trajectories in the fields of cephalopod fisheries and conservation (Xavier et al. 2015). Given all the above, we propose several interconnected ways evolutionary genomics can facilitate resolving some of the biological uncertainties that impede sound managing of cephalopods stocks.

Common octopus as a model for incorporating evolutionary perspective in cephalopod fisheries management

We propose here that the common octopus, with the scarce knowledge on species boundaries and populations structure, accumulated data on stock abundance

Box 3 Why use the common octopus as a model for introducing evolutionary management in cephalopod fisheries?

1. Unresolved taxonomic status, lack of data on stock identity and connectivity

The common octopus is one of the most ubiquitous and exploited octopus species in the world. There is accumulated knowledge of their biology, and the species has successfully been used in experimental ecological studies. However, ambiguous species identification, along with lack of data on population structure and connectivity across different spatial scales, hamper accurate stock definition, and pose a real threat of their ill management.

2. Environmental sensitivity drives population dynamics

High environmental dependence of all developmental stages makes common octopus populations sensitive to ecological perturbations, but also implies an important role of adaptive processes in their genetic makeup, their dynamics, and future viability. Deeper understanding of the interactions between overfishing, environmental stress and population trajectories becomes crucial these days, when market demands and global change threaten their existence in a cumulative manner.

3. Unsustainably fished populations and lack of stock assessment data and management measures

While fishery practice is more than ever turning towards cephalopods, stock assessment data on common octopus are scarce and uncomplete. Consequently, management decisions cannot be built upon the relevant scientific information. Moreover, for many exploited stocks, management measures are either completely lacking or are inadequate. Evident decline of *O. vulgaris* stocks in the Mediterranean Sea emphasizes their vulnerability to overfishing, and underlines the urging need to resolve the main drivers affecting their abundance, manage currently unregulated octopus populations, and adjust existing assessments methods and management practice.

4. Shared major life history traits with many cephalopods

High trophic position and important role of common octopus in ecosystem functioning, their main life history traits e.g. fast growth, short life span and semelparity, environmentally-driven development, and population dynamic are typical for many other cephalopod species (with a distinct exception of highly migratory behavior of adult squids). That indicates that the lessons learned on the *O. vulgaris* as a model for evolutionary-based management have potential for a wide-reaching and cross-specific tailored implementation.

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driven by environmental factors, rarely assessed or managed stocks, and for which strong indication of unsustainable fishery practice already exist (Box 1, Fig. 1), would be a suitable model to test changing the paradigm of cephalopods fisheries approach by incorporating evolutionary perspective in their assessment and management (Box 3).

How to make straightforward use of evolutionary genomics in cephalopod fishery assessment and management?

Define management units which correspond to biological reality

Evolutionary genomics provides insights that can aid in resolving taxonomic conflicts, stock identification and structure, as well as their connectivity, i.e. dispersal patterns and migration, which all have clear-cut management implications.

Identity at the species level

Cryptic species are common in many cephalopod groups (e.g. Bello 2019; Avendaño et al. 2020; Fernández-Álvarez et al. 2020; Tang et al. 2020; Xu et al. 2020). Such morphologically similar species often differ in life history traits and phenology (such as age-at-maturation or spawning period), which are commonly used in stock assessment and management (Domínguez-Contreras et al. 2018; Arkhipkin et al. 2020). Correct species identifications thus bear direct management consequences. To that end, regional or cooperative worldwide genomic analysis on the specific cephalopod species complex of interest could provide information on stocks taxonomic identity using even a limited number of samples per population (Tang et al. 2020).

Structure and connectivity at the population level

Population structure of most fishery important cephalopods is complex and often still unresolved (Rodhouse et al. 2014; Arkhipkin et al. 2020), and specific life history traits and phenotypic plasticity of cephalopods hamper the application of traditional tools in population

estimations (McKeown et al. 2019). However, genomic approaches offer readily employed tools to identify distinct stocks even in cases where traditional genetic tools show no structure (Vendrami et al. 2017). That would allow recognizing the mismatches between biological stocks and assessment and management units that can cause population decline (Pita et al. 2015a; Casey et al. 2016; Gonçalves da Silva et al. 2020; Mejía-Ruíz et al. 2020; Timm et al. 2020). If panmictic metapopulation is harvested differently in two or more geopolitical areas, those management practices will have interconnected effects, and new data indeed shows that catches of transboundary species decline faster (Palacios-Abrantes et al. 2020). In that case, cooperative and shared management scheme between the geopolitical entities is recommended (Cardinale et al. 2017). Likewise, genomic tools can aid in detection of mixed stocks (Mullins et al. 2018). This has further practical repercussions as joint assessment and management of unrecognized mixed stocks hampers obtaining accurate information on each of the stock status (Grewe et al. 2015), and might ultimately drive the overfishing of one of the stocks (Benestan 2019). Moreover, in the case of highly migratory squid species, genomic data could enable monitoring of migrations and correct identification of stocks independent of their geographical or temporal presence, or could facilitate locating spawning grounds. High resolution insights into connectivity of explored stocks can provide fishery assessment and management with information on stocks recruitment patterns, source-sink dynamics and demographic (in)dependence, and thus indirectly also on the long-term stock resilience due to replenishment upon local environmental perturbations (Waples and Naish 2009; Cisneros-Mata et al. 2019; Silva et al. 2019b; Cheng et al. 2020; Lee and O'Malley 2020; Mejía-Ruíz et al. 2020; Timm et al. 2020). In addition, obtained fine scale patterns of stock connectivity can be very useful in designing spatial management tools (Katsanevakis et al. 2011; Domínguez-Contreras et al. 2018).

Account for adaptive processes

Two clear practical implications emerge from comprehensions on the interplay of environmental factors and their selective force driving genomic adaptation that could be extracted from cephalopods seascape genomic studies:

Recognizing adaptive population divergence

Environmental pressures (e.g. salinity or temperature) can drive population differentiation hidden from the resolution of traditional neutral genetic markers (for references see "Exploring the evolutionary potential of exploited stocks" section), and such insights have direct effects on stock definition issues elaborated under "Structure and connectivity at the population level" section. In species with limited dispersal abilities locally adapted populations can be then pinpointed, which brings on direct management implications (Berry et al. 2020).

Understanding the impacts of environmental variation on cephalopod stocks dynamic

Detecting genomic adaptive patterns can further help resolving an important question that still remains open for many cephalopod taxa: the relative role of plastic and genetic processes underlying phenotypic patterns and population abundance, but can also elucidate the role of particular environmental factors and the strength of their transgenerational effect. Although immediate implementation of such knowledge is still challenging, it will aid in understanding the way environment shapes cephalopods stock dynamic. Experimental genomic studies could also be conducted to infer larval sensitivity to specific environmental variables (Pespeni et al. 2013), which would deepen our understanding of ecological barriers to their dispersal and warn on the consequences of environmental alterations on the levels of stock differentiation and abundance.

Use genomic tools as add-on in stock assessment and monitoring

At the point of many cephalopod fisheries being extensively harvested, evolutionary genomic research could be effectively mounted for assessing effective population size or even to reconstruct multi-generational population trajectories (temporal stock dynamic) using one-time sampling point (Lehnert et al. 2019; Marandel et al. 2020). The resulting data could be used by fishery scientists to apprehend the sensitivity of cephalopod stocks to overfishing and environmental disturbance, and inform the

management of particular stock's current and future risk of decline, as well as to pinpoint management units of special concern.

That said, we also need to underlie that the conversion of the scientific findings into usable knowledge and its implementation into management practice occurs across the science-policy interface through complex social interactions (Nguyen et al. 2018). This is by no means a straightforward path. In the case of evolutionary genomics, the gap in communication grows even larger. That's not only because the research is occasionally conducted to fit its own purpose, but also due to applicable knowledge sometimes being stated in specific scientific jargon, not readily understandable even to fishery scientists. However, several frameworks have been proposed to efficiently implement population genomics insights into management and conservation practice that rely, among others, on early exchange of ideas, building of professional relationships, effective communication, and mutual learning among all involved scientists and policymakers (Domingues et al. 2018; Holderegger et al. 2019; Bernos et al. 2020; Hohenlohe et al. 2020).

Conclusion and future perspectives

With the wealth of supporting scientific studies and available tools, scientists and authorities alike are starting to recognize the need for inclusion of evolutionary perspective into fisheries management, although the wider implementation of such methods is still proving to be challenging (Waples et al. 2008; Shafer et al. 2015; Casey et al. 2016; Baltazar-Soares et al. 2018). Nevertheless, there are some promising examples of management implementing evolutionary-based tools in fisheries monitoring around the globe. Genomic tools have, for instance been used to inform conservation and management of the Atlantic salmon (Aykanat et al. 2016; Bradbury et al. 2018) and cod (Dahle et al. 2018; Sinclair-Waters et al. 2018), as well as Chinook salmon in Alaska (Larson et al. 2014). Prominently, stock assessments incorporating estimates of genetic variability have become the norm in regulating multiple salmon stocks in the north-east Pacific (Dann et al. 2013; Flagg 2015), whose fisheries collapsed in the 70′s. Furthermore, in accordance with the precautionary approach, fishery management's focus should ultimately be on utilizing evolutionary insights for preservation of the viability of all exploited stocks, not just in an attempt to rescue obviously depleted ones.

NGS methods can be readily applied to obtain reliable information on populations genomic diversity and divergence in exploited marine species lacking existing genomic resources (e.g. Benestan et al. 2016). However, newly available annotated genome assemblies of two spotted octopus *Octopus bimaculoides* (Albertin et al. 2015), Hawaiian bobtail squid *Euprymna scolope* (Belcaid et al. 2019), elusive giant squid *Architeuthis dux* (da Fonseca et al. 2020), and long arm octopus *Octopus minor* (Kim et al. 2018), along with draft genome of *O. vulgaris* (Zarrella et al. 2019), promise to make further genomics research on cephalopod populations even more straightforward. Additionally, singular abilities like extensive RNA editing with selective advantage, and even linked to temperature adaptation, have been recently verified in octopuses (Garrett and Rosenthal 2012; Liscovitch-Brauer et al. 2017), opening new avenues to extend our understanding of acclimation and adaptation in cephalopods. As world fisheries continue to shift their focus towards cephalopods, and invertebrates in general, the lack of data on their stock identity, connectivity and evolutionary potential is the biggest constraint fishery management now faces. Hence, wider implementation of evolutionary based tools in cephalopod fisheries promises to facilitate their sustainable exploitation and to improve our understanding of their adaptive abilities in today's changing and threatened marine ecosystems.

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