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What is biological cultural heritage and why should we care about it? An example from Swedish rural landscapes and forests

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Abstract

There is currently a growing concern that biocultural heritage is threatened in many landscapes. This paper focuses on biological cultural heritage, broadly meaning biological cultural traces that are considered as heritage, but leaving out other aspects of the biocultural heritage concept. An operational definition of biological cultural heritage (BCH) is suggested, based on niche construction theory: "biological manifestations of culture, reflecting indirect or intentional effects, or domesticated landscapes, resulting from historical human niche construction". Some factors that influence recognition of BCH are discussed, using a comparison between Swedish open to semi-open vs. forested landscapes. While the former landscapes are generally associated with biological cultural values, BCH is generally over-looked in forests. Two main reasons for this are suggested: loss of cultural memory and a perception of forests as wilderness. A conclusion is that recognition of BCH is essential for guiding development of biological conservation programmes in forests, irrespective of whether the conservation goal is to focus on culturally impacted forests or to conserve what is considered as close to pristine forests. Furthermore, recognising BCH in forests will promote interest and learning of the history of forests and their values and will be informative for developing conservation programmes for all biota in forests, not only those that historically were favoured by culture. Hence, there is no inherent conflict between preserving relatively untouched forests and those with remaining traces of pre-industrial forest management. The recognition of BCH in forests will inspire and promote further integration of cultural and natural heritage research.

Keywords

Conservation biology, Domesticated landscapes, Niche construction, Semi-natural grasslands, Wilderness, Wood pastures

Introduction

There is currently a growing interest in conservation of cultural landscapes, motivated by a concern that values associated with these landscapes are eroding (e.g. Rössler 2006, Harrop 2007, UNESCO 2008, 2014, Agnoletti and Rotherham 2015). Cultural landscapes represent relationships amongst people, events and places through time (Taylor and Lennon 2011). They are "combined works of nature and man" (UNESCO 1972, Article 1) or, as stated in the European Landscape Convention (Council of Europe 2000), "an area as perceived by people whose character is the result of the action and interaction of natural and/or human factors". A concept that has attracted a lot of attention in this context is biocultural diversity and heritage incorporating and integrating both cultural and biological (and abiotic) aspects of landscapes (e.g. Pretty et al. 2009, Gavin et al. 2015, Rotherham 2015, Bridgewater 2017).

Biocultural diversity refers to the interface and relationship between biological and cultural diversity (e.g. Maffi 2005, Agnoletti and Rotherham 2015, Lennartsson et al. 2018). Although there are other related concepts, for example "ecodiversity" (Naveh 1998) and "ethnobiology" (Wolverton et al. 2014), biocultural diversity has become dominating in the discourse linking different aspects of cultural diversity with use of natural resources and for identifying how these links promote and maintain both cultural and biological diversity (Lennartsson et al. 2018).

Biocultural heritage is defined by UNESCO (2008, page 8) as "living organisms or habitats whose present features are due to cultural action in time and place". Cultural landscapes across the world, considered as outstanding, are protected under the UNESCO World Heritage Convention, particularly focusing on (i) clearly defined landscapes designed and created intentionally by humans, (ii) organically evolved landscapes, such as agricultural landscapes and (iii) associative cultural landscapes, e.g. religious and sacred landscapes (Rössler 2006, pages 335-336). UNESCO (2008, page 9) recognises several "areas of interdependencies" between biological and cultural diversity, thus forming the basis of biocultural heritage: language and linguistic diversity, material culture, knowledge and technology, modes of subsistence (which includes land use), economic relations, social relations and belief systems.

Biocultural heritage is often associated with indigenous people (e.g. Maffi 2005, Pretty et al. 2009, Wolverton et al. 2014, Gavin et al. 2015) and local rural communities (e.g. Galluzzi et al. 2010, Dahlström et al. 2013, Otero et al. 2013, Agnoletti et al. 2015, Cohen et al. 2015, Vallejo et al. 2015, Rangel-Landa et al. 2016). However, some authors suggest that the concept should be applied more broadly, for example, as expressed by Cocks and Wiersum (2014, pages 733–734) that biocultural heritage "…should be extended to include the values and associated practices concerning biodiversity of any kind of either traditional/rural or modernized/urban societies." This view is expressed also in the European Landscape Convention (Council of Europe 2000) which recognises "landscapes that may be considered outstanding as well as every-day and degraded landscapes". Furthermore, biocultural heritage usually reflects something "old and traditional". However, although the material basis of what is considered heritage often has deep historical roots, the meaning and value people assign to material manifestations of culture are considered constantly changing and renegotiated in the current society (e.g. Hobsbawn 1983, Smith 2006, Tilley 2006, Graham and Howard 2008, Storm 2008, del Mármol and Vaccaro 2015, Braaksma et al. 2016, Stenseke 2016). This also holds for biological manifestations of heritage, for example, features of species, species distributions or vegetation patterns, understood as having originated or having been favoured historically, e.g. by past management regimes. Furthermore, as biological manifestations of cultural history are living, they may survive, unchanged or transformed, although the historical cultural context where they originated has vanished (Eriksson 2016).

Given these considerations, there is a need for discussing and clarifying what kind of biological features that are recognised as heritage. At first, we should recognise that human impacts always leave biological traces. This is unavoidable and ubiquitous. Some of them are highly valued and some are not, because they are not recognised or because they are considered as degraded nature, uninteresting or ugly. Henceforth in this paper, a distinction is made, using the term "biological cultural heritage" as broadly meaning biological cultural traces (species, vegetation etc.) that are considered as heritage, but leaving out other aspects of culture (e.g. language, religion etc.) that are also part of the biocultural heritage concept.

The objectives of this paper are twofold. Firstly, an operational definition of the concept biological cultural heritage is suggested. Secondly, some factors that influence how biological cultural heritage is identified and perceived are discussed, using a comparison between two components of rural landscapes in Sweden: (i) open and semi-open landscapes with remains of (what are viewed as) traditionally managed semi-natural grasslands and (ii) forested landscapes. The rationale for this choice of landscape components is that open rural landscapes are generally associated with cultural values, whereas forests largely have become excluded from being seen as harbouring values related to cultural heritage. The objective is to try answering the question why this is so and thereby identifying some of the challenges associated with assigning biological features as heritage.

Biological Cultural Heritage – a suggested definition

Biological cultural heritage (henceforth BCH) has been defined as: "…ecosystems, habitats and species which have originated, developed or been favored by human utilization of the landscape and whose long-term persistence and development is dependent on, or favored by management." (Swedish National Heritage Board 2014). This definition is similar to, but more specific than the UNESCO (2008) definition of biocultural heritage as “living organisms or habitats whose present features are due to cultural action in time and place”, the latter leaving out any reference to long-term persistence. Both these definitions are rather broad and avoid any specification of the time-depth of the origin of the cultural actions, i.e. the human utilisation of the landscapes. Even features such as a clear-cutting in a production forest would be BCH according to these definitions.

Human cultural impacts always leave biological traces. A starting point is asking what kinds of biological cultural traces there are. I suggest we can recognise three levels of biological cultural traces, distinguished by an increasing magnitude of interaction with culture through history.

The first level is indirect effects of human actions. All kinds of human activities influence other species indirectly, by favouring some species, for example, by creating suitable habitats for them or by disfavouring some species, for example, by destroying their habitats. This is trivial, but may not preclude interesting biological legacies from human history. In a study of bracken (*Pteridium aquilinum*) in Finland, Oinonen (1967a) associated clones of different size with various war episodes going back to the 14th century. One example was an unusually large bracken clone, which Oinonen suggested was spatially associated with the raiding of a stronghold close to the present-day city of Turku in the year 1318. The proposed mechanism behind this and other examples of spatial associations between bracken clones and war episodes is that war promotes fires and fires promote recruitment of bracken. Of course, it was not the intention of the war episodes to promote bracken. However, given that we have some knowledge of the association between bracken clones and Finnish war history at the specific sites, we may regard these bracken clones as BCH.

The second level is biological cultural traces that reflect human intentionality affecting single species or groups of species. For example, Rotherham (2007) mentions what he calls botanical indicators of antiquity and disturbance, such as “working trees”. For example, in former wooded meadows, trees bear signs of earlier pollarding and coppicing (e.g. Hæggström 1992, 1998, Hartel et al. 2015). Other examples of biological cultural traces reflecting human intention are remnants of fruit trees or other plantations close to no longer existing farms and cottages (e.g. Gunnarsson 2010, Karlsson Strese et al. 2014). We may regard all these biological cultural traces as BCH.

Note that the second level partly incorporates the first level. Human intentionality, for example, in creating a garden or a wooded meadow, unavoidably implies indirect effects for other species. For example, the exceptional species richness of semi-natural grasslands such as wooded meadows with a long management history (Wilson et al. 2012, Eriksson and Cousins 2014) reflects both intentionality and indirect effects. We may regard the patterns of species composition and diversity, *per se*, in these former meadows, as BCH.

The third level is when the biological cultural traces are the result of long-term reciprocal interactions between culture and the biological communities that serve as a basis for the culture. These interactions create what has been called domesticated landscapes, broadly meaning whole landscapes transformed by humans to support society, but also affecting many other species (e.g. Terrell et al. 2003, Erickson 2006, Kareiva et al. 2007, Widgren 2012, Eriksson et al. 2018). Domesticated landscapes can be seen as the result of niche construction, a process whereby organisms, through their activities, modify their own and other species' niches (Odling-Smee et al. 2003). When humans are involved in a niche construction process, culture becomes one of the key factors (Kendal et al. 2011), creating a cultural niche (Laland and O'Brien 2012). Theory of human niche construction has been productive in understanding many features of human management and land-use, for example, global species distributions (e.g. Boivin et al. 2016), domestication of plants and animals (e.g. Smith 2016), development of infields (Eriksson and Arnell 2017) and for understanding the present anthropogenic biosphere in general (Ellis 2015).

Incorporating domesticated landscapes resulting from niche construction in a definition of BCH specifically stresses that biological cultural traces have or have had (previously during history) a great importance and meaning for people. Domesticated landscapes also relate to what has been termed "sociotechnical transition pathways" (Geels and Schot 2007). Furthermore, over time and due to the reciprocal interactions between culture and biological communities, both cultural and biological features have developed and changed. For example, management practices change over time, in response to and influencing the structure and composition of biological communities. What characterises this third level, domesticated landscapes, is that it encapsulates a "wholeness" of the environment influenced by and influencing human society. As such, it partly incorporates the previous two levels. Domesticated landscapes derived from niche construction processes include intentionality and unintended indirect effects on various species.

I thus propose the following definition of Biological Cultural Heritage (BCH): biological manifestations of culture, reflecting indirect or intentional effects or domesticated landscapes, resulting from historical human niche construction (Figure 1).

However, we need to clarify a critical question related to the definition. Heritage is not a value-neutral concept. As mentioned above, the meaning and value people assign to material manifestations of culture may change over time (e.g. Smith 2006, Graham and Howard 2008, Storm 2008, Braaksma et al. 2016) and cultural heritage generally has a positive connotation. A question is what makes BCH recognised and thus valued in a society?

There is extensive literature concerned with people's valuation of biological features and objects in landscapes. To cover this vast literature would be far beyond the scope of this paper, but it is nevertheless possible to identify some generalities. There are two main approaches to understand people's valuation and appreciation of biological features of landscapes: that preferences are culturally derived and biased or that they have an evolutionary basis (Fry et al. 2009). An example of the latter is the so called "savanna hypothesis", suggesting that humans have an innate preference for resource-rich, semi-open landscapes, with access to water bodies (Orians and Heerwagen 1992). For the purpose of this paper however, I leave this latter possibility out and henceforth focus on preferences reflecting culturally derived values.

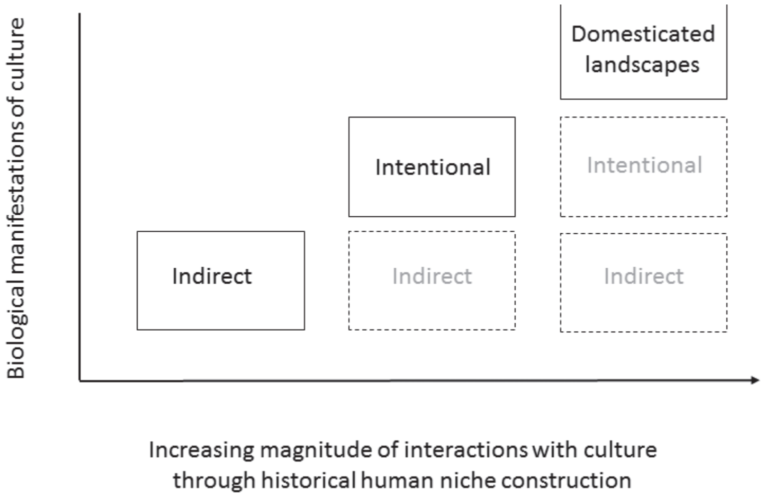

Figure 1. Biological cultural heritage defined as biological manifestations of culture, reflecting indirect or intentional effects or domesticated landscapes, resulting from historical human niche construction.

Generally, it is acknowledged that aspects such as landscape beauty, knowledge and memory of landscape history are important factors in valuation of landscapes (e.g. Schama 1995, Olick and Robbins 1998, Fairclough and Herring 2016). Herrington (2016) remarked that there has been a renewed interest in the concept of beauty during the last decades, in discourses on art, philosophy and landscape research. For landscapes, Herrington (2016, page 447) proposed that the most important aspects of beauty are "…contextual beauty and (…) functional beauty (which) both ask us to include the landscape's functional role in deeming a landscape beautiful." There is empirical support for this proposition when applied to landscapes (e.g. Vallejo et al. 2015, Dalglish and Leslie 2016). A possibility (so far very little studied) is that aesthetic preferences develop as a reciprocal interaction between humans and the physical, biological and cultural environments, an aesthetic niche construction process (Portera 2016). Furthermore, as remarked by Antrop (2005, page 21): "…the ability to tell a history of a place strongly enhances the identity and the overall value". This assumes that knowledge of landscape history and a "cultural memory" still exists. Potentially, landscapes may harbour biological (or other material) cultural traces that are not regarded as heritage, simply because of a loss of cultural memory (e.g. Rotherham 2007) or "cultural severance" (Rotherham 2013). An active and living knowledge and cultural memory relates to the current use of landscapes. This reflects the fact that the meaning and value people assign to material manifestations of culture relate to the extent people actually live on and work with the landscape (Buijs et al. 2006, Lindborg et al. 2009, Braaksma et al. 2016). This in turn reflects the importance of involvement of people when assessing values of landscapes and landscape features (e.g. Stenseke 2009, Svensson 2009, Dalglish and Leslie 2016).

These aspects of heritage may relate to both intangible and tangible values, in various ways linked to perceptions of continuity, private and public memories, identity and a sense of place (Taylor and Lennon 2011). The possibly strongest perception of heritage is when natural sites are regarded as sacred (e.g. Dudley et al. 2009, Allendorf et al. 2014, Jackson and Ormsby 2017).

Thus, in order to be recognised as biological cultural heritage (Figure 1), the following criteria should be fulfilled: (1) The biological cultural trace reflects either a previous (historical) human impact or a current impact which is rooted in what is currently considered as a tradition (whether "invented", *sensu* Hobsbawn (1983) or not). A time-depth, a history, is essential. (2) If the biological cultural trace no longer has a function or role, knowledge of its previous function or role is essential. (3) It is essential that the biological cultural trace evokes feelings, either due to its role for people's identity and sense of place or for its sanctity or sheer beauty.

An example: Swedish rural agricultural landscapes and forests

Background

"*Before the industrialization of agriculture, only rarely did one run a farm or raise cattle without the support of a forest.*" (Agnoletti and Santoro 2015, page 440)

The second objective of this paper was to compare BCH in two different components of rural landscapes in Sweden: (i) open and semi-open pastures and meadows and (ii) forests. As the above quote from Agnoletti and Santoro (2015) suggests, agriculture historically utilised open land, crop fields, pastures and meadows and forests. Today, these two kinds of landscape components are viewed differently when it comes to recognising and valuing biological features in the context of culture and history (Figure 2). The rationale for making this comparison here is thus that it serves to illustrate some of the problems and challenges associated with recognising BCH.

In the southern parts of Sweden, large-scale landscape transformations due to agriculture had previously commenced during the Neolithic (from ca. 3900 BCE, Welinder 2011) and continued and expanded during the Bronze and Iron Ages (Pedersen and Widgren 2011). Many agricultural areas still comprise cultural landscapes with a long uninterrupted history of human management (e.g. Berglund 1991, Eriksson and Cousins 2014). The deep historical roots of open and semi-open grassland dominated landscapes are well known, as well as in a broader European context (e.g. Odgaard and Rasmussen 2000, Berglund et al. 2008, Emanuelsson 2009, Poschlod and Baumann 2010, Eriksson 2013, Kuneš et al. 2015). These grasslands are highly valued for their biodiversity and receive considerable subsidies to maintain management by grazing or mowing (e.g. Veen et al. 2009, Council of Europe 2017). The importance of a long previous historical management for this biodiversity has been documented in several studies (e.g. Cousins and Eriksson 2002, Lindborg and Eriksson 2004, Helm et al. 2006, Gustavsson et al. 2007). The perception of these landscapes as BCH is uncontroversial (Figure 3) and holds for both nature conservation authorities, as well as for

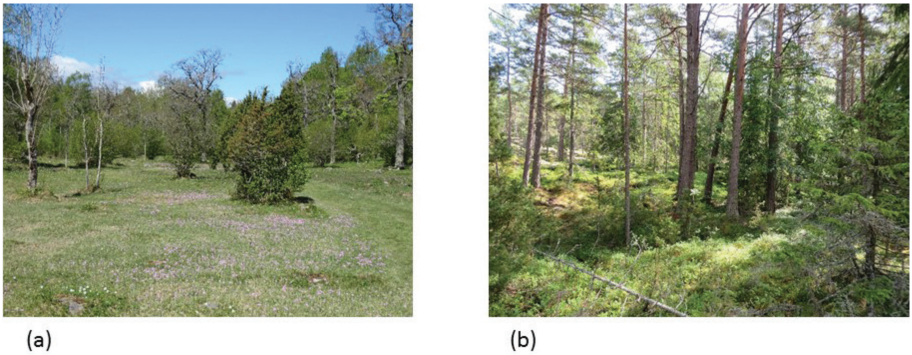

Figure 2. While remains of old agricultural management such as wooded meadows are viewed as cultural landscapes, forests usually are not. **a** Wooded meadow at Häverö parish, north of Stockholm, Sweden **b** Formerly grazed forest at Singö, north of Stockholm, Sweden. Photo: Ove Eriksson.

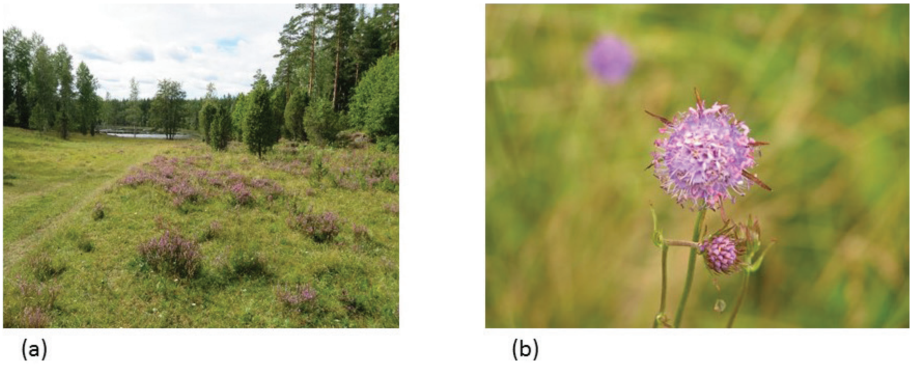

Figure 3. Biological cultural heritage may refer to a site where historical management has created species-rich grasslands, as well as to single species. **a** A semi-natural grassland at the Natura 2000 site of Stora Åsa, Province of Södermanland, Sweden. **b** *Succisa pratensis*, a species characteristic for these grasslands and which remains as legacy in forests long after management has ceased (Herben et al. 2006). Photo: Ove Eriksson.

people in general (e.g. Ihse and Lindahl 2000, Stenseke 2006, Lindborg et al. 2009, Eriksson and Cousins 2014, Eriksson 2016, Anonymous 2017a).

This is in stark contrast to how forests are perceived, not only in Sweden, but throughout Europe. As remarked by several authors (e.g. Rotherham 2007, 2015, Agnoletti and Santoro 2015), conservation biologists, ecologist and foresters often fail to appreciate forests as cultural landscapes. As succinctly stated by Agnoletti and Santoro (2015, pages 438-439): for forests there is a "widespread application of an idea of 'naturalness' (…) informed by the 'degradation' paradigm, emphasizing the negative role of man". Steen (1958) summarised the debate on forest grazing in Sweden during the early 20th century and despite recognising that forest grazing historically has promoted species richness in forests, he presented an overly negative view on forest grazing, mainly from a forestry perspective (see also Kardell 2016). This perspective is still dominant. For example, "During the 18th and 19th centuries, many forests were heavily over-exploited for farming, housing construction, wood for fuel, charcoal for the iron industry (…) Cattle grazed the forests hampering tree regeneration." (Swedish Forest Agency 2015). Clearly, the basic attitude is that human impacts before modern forestry were degrading forests. To clarify, it may well be correct that forest grazing truly hampers forest production. My point concerns how forests are valued from a cultural and historical perspective. I am unaware of any authority claiming that, for example, historical hay-making in wooded meadows degraded these systems and this is irrespective of whether one may truly regard wooded meadows as degraded former deciduous forests. Accordingly, in many forested ecosystems, conservation programmes focus on recreating natural disturbance regimes with the goal to maintain or restore wilderness, overlooking and downgrading historical cultural impact of humans (e.g. Holl and Smith 2007, Svensson 2009, Olwig 2016). Furthermore, they often wrongly interpret culturally impacted forests as untouched (e.g. Willis et al. 2004, Josefsson et al. 2009, Latałowa et al. 2015).

Some may claim that the paragraph above is like attacking a straw man. For example, cultural heritage is indeed mentioned briefly in the Swedish Environmental Objective for Sustainable Forests (Anonymous 2017a). In the instructions for surveys of forest key biotopes, culturally influenced biotopes are included (Swedish Forest Agency 2014). However, they only appear under a special sub-heading ("Biotopes formed by management"), distinguished from coniferous, deciduous and wet forests, which then, by implication, are not formed by cultural impact. In a recent report from the European Academies Science Advisory Council on "Multi-functionality and sustainability in the European Union's forests" (EASAC 2017), cultural heritage and services are mentioned a few times but not explored much and, overall, the report argued for a "pre-degradation baseline" when assessing biodiversity change. In a review of how legislation and certification of forests influence biodiversity, there were no discussion of values associated with historical cultural influences on biodiversity (Johansson et al. 2013) and the same bypassing of cultural impacts holds for some overviews of so-called "retention forestry" (Gustafsson and Perhans 2010, Gustafsson et al. 2012). In Swedish forestry conservation debates from the 1960s and onwards, aspects of cultural history are generally absent (Simonsson et al. 2015). A recent study of stakeholder's preferences regarding various features of forests, based on questionnaires (Nordén et al. 2017), did not even include any question of cultural values. A general conclusion is that explicit references to cultural values of forests are conspicuous by their absence. Some figures are illustrative. The total area in Sweden of protected grazed forest is ca. 290 hectares (Anonymous 2017b) and of the approximately 100,000 hectares of semi-natural grasslands in Sweden currently receiving subsidies for maintaining grazing management to preserve biological and cultural values, ca. 2% is grazed forest (Swedish Board of Agriculture 2012).

Biological cultural traces in forests

The difference between these two rural landscape components in how historical cultural impacts are perceived, i.e. downgrading forests as cultural landscapes, is not due to a paucity of scientific evidence on forest history. The existence of legacies of pre-modern long-term cultural impact in boreal, boreo-nemoral (Sjörs 1999) and temperate forests in the northern hemisphere is well-known (e.g. Foster 1992, Lindbladh 1999, Rackham 2003, Bradshaw 2004, Hermy and Verheyen 2007, Müllerová et al. 2014, Kirby and Watkins 2015). Vast areas in Europe were historically used as wood pastures (Hartel et al. 2015, Plieninger et al. 2015) and for collection of livestock fodder (e.g. Slotte 2001, Müllerová et al. 2014).

In southern and central Sweden, most area of what is now forest has for long and, until the late 19th to mid-20th centuries, been used for grazing and hay-making (e.g. Slotte 2001, Segerström and Emanuelsson 2002, Brunet et al. 2012, Eriksson and Cousins 2014, Cousins et al. 2015, Kardell 2016). From medieval times, mining became important in parts of southern and central Sweden and had an enormous impact on forests due to the demands for firewood and charcoal (e.g. Emanuelsson and Segerstrom 2002, Angelstam et al. 2013). The wide stretches of forests in the interior of central and northern Sweden also have a long history of human influence. Lindholm et al. (2013) reviewed evidence of numerous archaeological sites in the forested inland of Sweden, related to game pitfalls, village outfield pasture, tar and charcoal production, small mills, hay-meadows and shielings. From around AD 300 and onwards, this part of Sweden was part of integrated trade networks (e.g. Ashby et al. 2015, Lindholm and Ljungkvist 2016) and the collective impact suggests that the forested inland was colonised and utilised from the first centuries AD, much earlier than previously thought. In fact, agriculture may have reached these areas already during the Neolithic and Bronze Age (Josefsson et al. 2014) and, certainly, from the Roman Iron Age, ca. AD 100-500 (e.g. Karlsson et al. 2010). Lindholm et al. (2013) concluded that this cultural landscape has been generally overlooked, both from historical and biological viewpoints. In the northern boreal forest, Sami people practised agriculture, with hay-making, livestock grazing, including reindeer grazing in pine forests, at least from 300-400 years BP (Josefsson et al. 2009, Josefsson et al. 2010a, b, Rautio et al. 2016). During the 16th century, there was a large immigration of Finnish settlers to central Sweden, practising slash-and-burn agriculture and livestock herding (e.g. Linder and Östlund 1998, Wedin 2004). An impact of former land use is evident even in forests that have been considered pristine, e.g. boreal swamp forests (Hörnberg et al. 1998), old spruce forests (Bradshaw and Hannon 1992) and northern boreal forests (Josefsson et al. 2009, Josefsson et al. 2010a).

Furthermore, the difference between these two rural landscape components in how cultural historical impacts are perceived is not due to general differences in recent land use history. Both open and semi-open rural landscapes and forests have been subjected to major land-use change over the last 150 years. From the late 19th century and onwards, the Swedish agricultural and forest landscapes underwent drastic changes

(Antonsson and Jansson 2011, Cousins et al. 2015). In agriculture, a range of new techniques were introduced (Morell 2011), resulting in abandonment of semi-natural meadows, which were transformed into arable fields, forest plantations or were left unmanaged, resulting in a succession towards forest (e.g. Emanuelsson 2009, Brunet et al. 2012, Eriksson and Cousins 2014). Although some meadows were used as pastures, the area of semi-natural grasslands has declined by more than 90% during the last century (Cousins et al. 2007, Cousins and Eriksson 2008, Cousins et al. 2015). Forest grazing was successively abandoned (Steen 1958, Kardell 2016). Initially, old and large trees were selectively harvested (e.g. Linder and Östlund 1998), but clear-cutting was introduced gradually during early 20th century, although selective cutting persisted until the 1950s (Lundmark et al. 2013). In general, this altered management resulted in a great increase in wood biomass and a new (younger) age structure of forests. For example, in an area in the province of Dalarna, estimates suggest an almost six-fold (from ca. 12 m^3/ha to 66 m^3/ha) increase in wood biomass between 1907 and 1989 (Ericsson et al. 2000). Norway spruce became increasingly dominant from the early 20th century (Lindbladh et al. 2014), currently making up 40% of the forest standing volume (Swedish Forest Agency 2015). Today, Sweden is a forested country: 57% of the area is productive forest, 12% is unproductive forest and 6% is other wooded land (Swedish Forest Agency 2015).

Overall, these changes reflect the transformation of Sweden from a mainly agricultural to an industrialised country. Some figures are presented to illustrate this change as follows: between the 1870s and the 1940s, the fraction of Swedish BNP coming from agriculture dropped from 40% to 10%, the number of crofters dropped from 100,000 to a few thousand and, while the number of farms remained more or less constant until the 1940s, this number declined drastically after the Second World War (Morell 2011). As discussed further below, these changes are associated with new perceptions for cultural values in forests.

The most general human impact on forests before this modernisation was through grazing by livestock, collection of hay at sites where this was suitable, selective use of wood and altered fire regimes (e.g. by slash-and-burn cultivation). This created an increased openness, promoting development of stands of old trees, particularly Scots pine, with a field layer of grasses and herbs (e.g. Segerström and Emanuelsson 2002, Josefsson et al. 2009). Close to settlements, the effects also included nutrient dynamics, soil compaction and increased microbial decomposer activity (Freschet et al. 2014). As stated by Ericsson et al. (2000, page 235): “This grazed forest with large Scots pines, grass and herbaceous plants constitute a landscape almost unknown today…”.

However, although old-fashioned ways of using forest do not exist anymore, the biological cultural traces have not gone. These legacies may refer to occurrences of deciduous forest stands in boreo-nemoral and boreal regions (e.g. Björsne and Bradshaw 1998, Hellberg et al. 2003), remaining patterns of species distribution (e.g. Lindbladh et al. 2000, Segerström and Emanuelsson 2002, Östlund et al. 2015) and culturally modified trees. Trees with traces of ringbarking, production of axe-handles, boundary marks and trees for magic use are abundant in northern Sweden (Östlund et al. 2002, Rautio et al. 2014). Some trees bear written messages, a kind of forest notice board (Andersson et al. 2005). Many plant species may persist as slowly declining populations over quite long time. In grassland systems, time lags in the order of a century have been documented (Lindborg and Eriksson 2004, Helm et al. 2006) and legacies of previous grassland management in what is currently forest and maintained over a century, have been documented (Herben et al. 2006, Johansson et al. 2011). These legacies may also remain after one forest-cycle of clear-cutting (Jonason et al. 2016). Very few similar studies have been conducted in forest systems and focusing on what is regarded as forest species, perhaps due to a preconceived notion that such legacies are not expected when research is conducted in forests. Suggested examples of species reflecting previous cultural impacts in forests include plants such as *Actaea spicata*, *Lathyrus vernus*, *Galium odoratum* and *Festuca altissima* (Nilsson et al. 2001), *Lycopodium complanatum* (Oinonen 1967b) and *Chimaphila umbellata* (Lundell et al. 2015), lichens such as *Lobaria* spp. (Nilsson et al. 2001) and *Usnea longissima* (Josefsson et al. 2005), wood-dependent beetles (Lindbladh et al. 2003) and birds such as *Dendrocopos minor* (Lesser spotted woodpecker) (Wiktander et al. 2001) and *Caprimulgis europaeus* (Nightjar), *Lullula arborea* (Wood lark) and *Dryocopus martinus* (Black woodpecker) (Linder and Östlund 1998). Despite these suggested examples, there is a general paucity of studies of historical land-use effects for species of plants and animals in forests, as compared to semi-natural grasslands (cf. Eriksson and Cousins 2014).

Thus, there is no doubt that forests in Sweden are indeed a historical cultural landscape and that there are abundant legacies of previous management. Modern forestry has not eroded all biological cultural traces emanating from the time before modernisation.

I suggest that there are two main reasons why BCH is generally over-looked in forests; loss of cultural memory and the dominance of a perception of forests as wilderness. In the following sections, I discuss these in some more detail.

Loss of cultural memory

Cultural memory (synonymous to “social memory”, Connerton 1989) is a concept used in various contexts within the social sciences (e.g. Hirsch and Smith 2002, Terry 2013). According to Connerton (1989, page 37), social memory works when “groups provide individuals with frameworks within which their memories are localized (…) mental spaces provided by the group (…) these mental spaces (…) always receive support from and refer back to the material spaces that particular groups occupy.” Laland and Rendell (2013) suggested that cultural memory is a general feature of humans, based on knowledge transmission, learning and copying. Furthermore, they considered cultural memory as adaptive for coping with changing environments. This is in line with a definition of culture as “information that is acquired from other individuals via social transmission mechanisms such as imitation, teaching, or language” (Mesoudi 2011, page 2). An example of the association between cultural memory and material manifestations of culture is the common understanding that in pre-literate societies, material features of whole landscapes such as settlements with their surrounding resource base (crop fields, pastures etc.), graves and ceremonial sites were organised to represent people's perceptions of cosmology and religion, their 'world view' (e.g. Hodder 1990, Tilley 1994, Kristiansen and Larsson 2005, page 357 ff., Andrén 2014).

It may seem far-fetched to envisage anything similar in a modern society. However, the discourse on perceptions of heritage, as founded by knowledge and memory of landscape history, identity and sense of place and the meaning people attribute to material remains of history (e.g. Schama 1995, Antrop 2005, Taylor and Lennon 2011, Braaksma et al. 2016), in a way reflects a similar role of landscapes for people today. By "knowing the landscape", people may experience home and identity. Knowing the historical background of places or features of landscapes promotes such feelings, respect for previous generations and it stimulates an active interest in maintaining features regarded as traditional. Consider a farmer who is managing a semi-natural grassland previously managed over many generations. By doing this, the farmer maintains a cultural memory of management history and this cultural memory adds to the perceived heritage value of that particular grassland. This example illustrates cultural memory founded on ongoing activity. Indeed, studies of people's valuation of agricultural rural landscapes suggest not only that a cultural memory promotes perceptions of heritage values, but also that such a cultural memory partly depends on the current utility of these landscape elements (e.g. Stenseke 2006, 2009, Braaksma et al. 2016).

Although the loss of biological and cultural values due to drastic landscape changes was subject to debate in Sweden from the 1930s and onwards, it was not until the 1980s when a national survey of semi-natural grasslands was initiated (Swedish Environmental Protection Agency 1987). Such national programmes for preserving BCH in agricultural landscapes play an important role for promoting a societal cultural memory. These programmes represent what Smith (2006) termed an "authorized heritage discourse", i.e. "… aesthetically pleasing material objects, sites, places and/or landscapes that current generations 'must' care for, protect and revere so that they may be passed to (…) future generations (…) to forge a sense of common identity based on the past" (Smith 2006, page 29). In addition, a societal cultural memory also depends on perceptions of people who are not themselves directly close to the material cultural manifestation (for example, they live in cities and have their main experience of the rural agricultural landscapes from books and television or perhaps from short visits during holidays). Thus, popular culture plays a role. For example, the Swedish author of children's books, Astrid Lindgren (e.g. 'The six Bullerby Children', 'Emil of Lönneberga') has probably meant a lot for Swedish people's appreciation of old-fashioned rural agricultural landscapes and for maintaining a cultural memory even amongst those lacking direct experience of such landscapes.

In contrast, forested landscapes fall outside this authorised cultural heritage discourse (e.g. Svensson et al. 2018). The separation of agriculture from forest management during the 20th century (mainly by abandonment of forest grazing and haymaking on wetlands) initiated a loss of cultural memory of forests as old cultural landscapes. Forests became an object for the forestry industry. Rural people's livelihood did not depend on forests as previously. There were few people transmitting memory of previous cultural practices in forests. In fact, from the 1950s, a large fraction of people, living in agricultural regions outside the most agriculturally productive plains, left for other jobs in the industry (Morell 2011). A similar separation holds for industry historically dependent on forests. It is illustrative that some of the industrial remains of the mining landscapes in Sweden are protected as UNESCO World Heritage (The Mining Area of the Great Copper Mountain in Falun and the Engelsberg Ironworks), but not the forest landscape that was an essential basis for the industry.

Thus, the divorce between agriculture and forests that commenced during late 19th century and was, more or less, completed in the 1950s, resulted in a general loss of cultural memory regarding forests. This loss of cultural memory concerned people living in the rural landscapes as well as authorities concerned with management and conservation. In contrast, a cultural memory was maintained in agriculture, implying that remains of old and traditionally managed grasslands were perceived as cultural heritage and their biological features thus as BCH.

Instead of being viewed as cultural heritage, conservation efforts in forests focused on protecting wilderness, which was seen as not (yet) exploited by the forestry industry. This leads to the other main issue influencing why BCH is over-looked in forests, how wilderness is understood and perceived.

Perceptions of wilderness

There is extensive literature on the history of the conceptual divide between culture and nature (e.g. Williams 1980, Worster 1994, Haila 2000, Kricher 2009). Here it may suffice to remark that, during the Enlightenment (late 1600s - 1700s), a view developed where nature was represented as an object of exploitation and investigation, inspired by a Cartesian idea of the world as a machine (Haila 2000, Outram 2013). For example, Williams (1980) suggested that the conceptual separation of culture vs. nature was a result of the identification of humans as free to investigate and make experiments on nature. During the late 1700s and especially during the following century, a critical reaction emerged to what was regarded as a destructive human dominance over nature. This was a feature of what has been termed "Romanticism", which promoted a view that nature represents something not artificial, authentic, uncorrupted and good, as a state opposed to civilisation (Outram 2013).

One such influential author was the explorer and naturalist Alexander von Humboldt, whose books were widely read (e.g. *Ansichten der Nature*, in English translation *Views of Nature*, von Humboldt (2014 [1808]). Von Humboldt had an impact on the development of an early green movement (e.g. Henry David Thoreau) and on the proponents for establishing National Parks in the United States, such as John Muir (Wulf 2015). During late 19th century, ideas of national heritage also developed in many other countries along with an ambition to consolidate national identification (e.g. Schama 1995, Smith 2006, Graham and Howard 2008). Natural (and cultural) heritage became a "thing" that was conceptually possible to preserve, to freeze in a certain state (Olwig 1984). In Sweden, the first National Parks were established 1909. The underlying idea was to preserve wild nature, considered as representing what was seen as characteristic for Sweden as a nation (e.g. Mels 1999).

The National Parks in Sweden also included areas that were strongly influenced by management. An example of this is Ängsö, an island north of Stockholm, composed of open pastures and semi-open wooded meadows. This vegetation was initially interpreted as remnants of old virgin deciduous woodland. As nature protection prescribed free development, excluding human intervention, the wooded meadows at Ängsö soon encroached and the original beauty deteriorated. During the following decades and after a debate amongst conservationists, management was reintroduced at Ängsö in the 1940s. Using the concept suggested in this paper, one could say that BCH was finally recognised. However, although several early conservationists argued that, not only the still managed agricultural landscape, but also forests should be seen as products of culture (thus being BCH), nature conservation was henceforth mostly concerned with wilderness (this debate is described in Gren (2010) and Wijkander (2017), both being only available in Swedish).

An idea underlying the early movement to protect nature was that human intervention in nature is fundamentally destructive and that wilderness (the object of preservation) is not compatible with cultural impacts. This is still a common opinion. As succinctly stated by Stokes (2018, page 2): "This idea of wilderness as antidote to civilization serves as a central organizing principle of the modern conservation movement (…)." Questioning the existence of wilderness would then be seen as threatening the whole idea of nature conservation. As illustrated by the debate following a controversial paper by Cronon (1996), where he argued that wilderness is a human social construct, there is much confusion associated with the wilderness concept (Proctor 1998). The question of how wilderness is conceptually understood should not be confused with the issue of whether those presumed wilderness-areas really are untouched by humans. The issue is not whether nature is or is not, truly pristine (most vegetation is not, e.g. Willis et al. 2004), but rather if and when an idea of a wilderness is projected on nature and in what sense such a projection implies certain values and actions. Cronon was thus misinterpreted, as if he had claimed that wild nature *per se* does not exist. This was of course not the point. Very few, if any, hard-core social constructivists would claim that. It is the concept of wilderness that is a social construct, not the physical objects that build up nature (e.g. mountains, forests, species). The conceptual relationship between culture and nature is still underlying controversies revolving around the so-called "new conservation science" (Marris 2011, Kareiva and Marvier 2012, Doak et al. 2014, Wuerthner et al. 2014), although some authors argue that these contrasting opinions may quite easily be reconciled (e.g. Mace 2014).

It is thus argued that the association of nature worthy of protection with the concept wilderness, understood as nature where there has been no cultural impact, has contributed to inhibit recognition of BCH in forests, i.e. created a kind of blind spot for forests as cultural landscapes. While rural agricultural landscapes escaped the conception of wilderness, but remained being valued as cultural landscapes and also valued for the biological diversity, conservation of forests still maintained the original 19th century focus on what was perceived as wilderness.

Discussion

The growing interest in conservation of cultural landscapes reflects the fact that many old cultural landscapes are threatened, but also an awareness that cultural landscapes may be biologically rich. In a world of ever increasing human dominance, it is important to gain knowledge of how this biological richness has developed and could be maintained. Along with this interest, there is also an ambition to promote integration between research and programmes for cultural and natural heritage (Gillson and Willis 2004, Swedish National Heritage Board 2014, Anonymous 2017a, Crumley et al. 2018). For too long, these two fields have been separated in both academia and institutions, such a governmental authorities responsible for organising and managing heritage (including biological diversity). An important step to achieve such integration is to agree on concepts used in communication and research (e.g. Eriksson et al. 2018). I suggest that the proposed definition of biological cultural heritage (biological manifestations of culture, reflecting indirect or intentional effects or domesticated landscapes, resulting from historical human niche construction) will be helpful to promote such integration and a research agenda for studies of biological cultural heritage in general and thus to guide management programmes in cultural landscapes. This definition identifies different forms of relationship between biological features and culture, arranged in a gradient of increasing intensity of interactions between the focal biological features and culture. The concept of domesticated landscapes formed by niche construction provides a theoretical framework for identifying mechanisms behind interactions between culture and biological features (e.g. Laland and O'Brien 2012, Eriksson et al. 2018), interactions that are embedded in complex networks, entanglements (Hodder 2012, Eriksson and Arnell 2017) or "biodiversification" (Cevasco et al. 2015).

The second objective of this paper was to try to identify factors influencing when and why biological cultural heritage is recognised. The method was to compare two components of rural landscapes in Sweden, open and semi-open landscapes and forested landscapes, which differ in the way they are perceived as cultural landscapes.

The starting-point was that biological cultural heritage is generally over-looked in forests. I suggest that there are two main factors responsible for this. Firstly, recognition and valuation as heritage depends on social context, specifically relating to current activities by people, people's perceptions of identity and sense of place, knowledge of history and a cultural memory both amongst people in general and amongst authorities. Concerning forests, there has been a loss of cultural memory (both locally and amongst authorities). This illustrates that recognising biological cultural heritage does not rely only on the biological features *per se* or on scientific knowledge of their historical background. Despite a solid scientific knowledge of the history of forest landscapes, biological cultural heritage is nevertheless over-looked. Secondly, basic assumptions and perceptions of a culture vs. nature divide, that emanated during the 19th century as a part of Romanticism have had and still have, a pervasive influence on perceptions and valuation of forests. Together, these two factors contribute to create a blind spot for cultural heritage in forests.

What are the implications of this conclusion? Why should we care about biological cultural heritage in forests? After all, if, as several authors claim, the meaning and value people assign to material manifestations of culture are constantly changing and renegotiated in the current society (e.g. Hobsbawn 1983, Smith 2006, Graham and Howard 2008), i.e. heritage is a social construction, is not the loss of cultural memory regarding forests just a reflection of such a renegotiation? In the current society, forests are either managed for industrial production or, as a recent addition to management objectives, climate change mitigation (e.g. EASAC 2017) or for conservation of biodiversity. With the latter aim in mind, the perception of forests as wilderness may perhaps work perfectly well.

I think there is a two-part answer to the question why we ought to care about biological cultural heritage in forests. The first part of the answer is "philosophical" and the second is pragmatic.

The discourse on how to value heritage revolves around the question of value relativism, i.e. whether there is or is not, an absolute point of reference or frame, for assessing value to tangible and intangible manifestations of culture. In the context of biological conservation, such a reference point is usually termed a baseline. Some argue that there are such baselines and one obvious choice would be untouched nature. For example, according to EASAC (2017), the pre-degradation state (note the negative connotation in the choice of term) of forests is such a baseline, suggested to be independent of societal values. This idea is also underlying arguments that conservation biology should prioritise preserving wilderness over conservation of cultural landscapes (e.g. Wuerthner et al. 2014). Others argue that baselines are always socially constructed (e.g. Hilding-Rydevik et al. 2018). The latter argument seemingly fits, on scientific grounds, into the reasonable conclusion that the forests we discuss here are indeed historical cultural landscapes and that the untouched state does not exist anymore. The view that baselines are social constructs may seem to imply that what we chose as a baseline would be principally arbitrary. Some conservationists have expressed worries for using this way of handling baselines, the "shifting baseline syndrome", i.e. when human perceptions of change guide conservation management (Pauly 1995, Papworth et al. 2009).

However, as remarked above, by referring to papers by Cronon (1996) and Proctor (1998), I would argue that the discussion on social construction in relation to biological features is somewhat confused. While the understanding and meaning we project on biological objects and features (such as a forest, a wooded meadow or a species) may well be socially constructed, these objects and features as such are, of course, objectively real. A reflection is that a focus on species instead of whole communities and ecosystems would alleviate the problems associated with whether nature as a whole is untouched or not. Most species are untouched in the sense of not being domesticated. Then it becomes an empirical question whether a focal species (or a group of species) has been favoured by or even dependent on historical cultural impacts. If this is the case, elements of cultural landscapes, for example a wood pasture or a wooded meadow, also represent a baseline that is not arbitrary.

This leads over to the second, pragmatic, part of the answer to the question why we ought to care about biological cultural heritage, namely that a multitude of biological features and objects in forests, including many species, actually were favoured by and even dependent on the historical cultural landscape (e.g. Björsne and Bradshaw 1998, Josefsson et al. 2009, Rotherham 2015, Agnoletti and Santoro 2015, Whitlock et al. 2017, references above in the Section "Biological cultural traces in forests"). In other words, these features and objects reflect the processes included in the definition of biological cultural heritage, indirect and intentional effects and historic landscape domestication, driven by human niche construction. Thus, conservation management of forests needs to incorporate knowledge of cultural history and this necessitates that biological cultural heritage in forests is recognised. As remarked earlier in this paper, research on species as historical cultural legacies in forests is a particularly neglected research field.

A recognition of biological cultural heritage is thus important irrespective of whether the conservation goal is to focus on culturally impacted forests or to try identifying what is considered as (or close to) a pristine state of forests (e.g. Samojlik et al. 2016). There is no inherent conflict between preserving relatively untouched forests and those with remaining traces of pre-industrial forest management. Consequently, even if it is true that biological cultural heritage is over-looked in forests, this does not imply that it is "wrong" to protect forests that have not yet been exploited by modern forestry. Given the current state for many threatened species, this may be highly motivated (e.g. Nilsson et al. 2001, Johansson et al. 2013).

In conclusion, it is argued that removing the blind spot for cultural history is essential for guiding development of both cultural and biological conservation programmes in forests. The notion of a blind spot for cultural history of forests should not be understood as criticism of the ambition to increase the forest area protected from modern forestry. However, it implies that features of previously culturally impacted forests should be recognised, for example, in restoration programmes. Furthermore, recognising and appreciating biological cultural heritage in forests will promote interest and learning of the history of forests and their values and will be informative for developing sustainable conservation programmes for all biota in forests, not only those that historically were favoured by culture. Finally, recognition of biological cultural heritage in forests will inspire and promote further integration of cultural and natural heritage research.

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RESEARCH ARTICLE

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Modification of landscape as promoter of change in structure and taxonomic diversity of reptile´s communities: an example in tropical landscape in the central region of Mexico

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Abstract

The degree of species loss was assessed by comparing the structure of communities and species diversity of reptiles from three different environments, one natural (tropical evergreen forest [TEF]) and two modified (shaded coffee plantation [SCP] and grazing area [GA]) from the mid portion of the Sierra Madre Oriental, Mexico. The results showed 29 species, 18 in TEF, 13 in SCP and 12 in GA. According to the abundance of each species, the reptile structure for TEF and SCP was similar and they both differed from GA, while the diversity (effective number of species) was the highest for TEF. The percentage of number of species from TEF accounted for 28% more species than SCP and GA, which indicated a species loss of about 70% in disturbed environments. The values of beta diversity were the highest between TEF and GA, followed by SCP and GA and to a lesser degree between TEF and SCP, which indicates that TEF showed a high number of exclusive species. Our results suggest that carrying out long-term studies that include richness and diversity in environments with different levels of disturbance, in addition to including characteristics of natural history, might enhance the development of more efficient conservation strategies for these species.

Keywords

Alpha diversity, beta diversity, conservation, disturbed environments, taxonomic diversity

Introduction

The development of agriculture and livestock activities has generated a high loss of original vegetation in diverse ecosystems of the world (Cayuela et al. 2006, Barragán et al. 2011). The tropical environments have been the most threatened, notably reducing their territorial extension (Sodhi et al. 2010) and diminishing the biodiversity of these environments (Kurz et al. 2014, Zhang et al. 2014). Amongst the main causes in the loss of territorial extension and, therefore, its biodiversity, are those caused by the anthropogenic effect, such as the change of land use or fragmentation of the landscape (Vié et al. 2009).

In tropical environments, the decline has been documented for many biological groups, such as arthropods (Benítez-Malvido et al. 2016), amphibians (Pineda et al. 2005, Pineda and Halffter 2004, Cruz-Elizalde et al. 2016), mammals (Garmendia et al. 2013), birds (Sekercioglu et al. 2004) and reptiles (Gibbons et al. 2000, Berriozabal-Islas et al. 2017). Additionally, it has been noted that modified environments negatively affect ecological interactions, as well as in survival rates, population growth, gene flow amongst populations and behaviour of individuals (Jones 1981, Dixo et al. 2009).

Changes in landscape structure influence the conformation of biological communities amongst sites (Pereyra et al. 2018), modifying their structure and the relative abundances of the species. An example of this, is the group of reptiles, which, due to their ecological and physiological characteristics, limited home ranges or the low vagility of their species, are highly sensitive to changes in the environment where they occur (Kurz et al. 2014, Berriozabal-Islas et al. 2017). Despite some studies registering that the richness of reptile species decreases as natural environments are transformed into cultivated areas or urbanised environments (Faria et al. 2007, Gardner et al. 2007), several other studies show that the surrounding matrix can maintain a richness similar to the fragments of original vegetation (Urbina-Cardona et al. 2006). For example, Suazo-Ortuño et al. (2008) found that lizards showed a high preference for disturbed areas (farming and grazing areas). These authors reported a steady increase in population size for two consecutive years of sampling and their conclusion was that anthropogenic disturbance in some circumstances might be a positive factor for some species and negative for others.

In Mexico, tropical forest remnants and transformed environments, such as agricultural and grazing areas make up the current landscape of some biogeographic regions (Hernández-Ruedas et al. 2014). An example of these is the Sierra Madre Oriental located in central Mexico, which is one of the provinces with most species richness and endemism for diverse biological groups such as amphibians, reptiles, plants, mammals and birds (Canseco-Márquez et al. 2004). However, most of area of this province has been strongly affected by human disturbance (Castro-Navarro et al. 2017). Based on the previous theoretical context and on the landscape change affecting the composition of biological communities through time and for multiple ecological relationships, many reptile species associated with the native vegetation are usually very sensitive to habitat disturbance (Berriozabal-Islas et al. 2017). Subsequently, it makes them useful as indicators of environmental health; for example, richness and relative abundance of species are good indicators for the status of an ecosystem (Semlitsch and Bodie 2003). Therefore and considering that reptiles are bioindicator groups of habitat disturbance (Suazo-Ortuño et al. 2008), in this study, we expected to find a pattern of change in community composition amongst environments, particularly species loss due to the transformation of their environment, change in relative abundance of species by the environment, high values of beta diversity as well as low taxonomic diversity in transformed environments.

We anticipated a high richness and species diversity in a native environment (tropical evergreen forest), compared to two transformed environments (shaded coffee plantation and grazing areas). In addition, we predict a loss of species from native evergreen forest to transformed environments due to turnover of species (i.e. changes in species composition amongst local assemblages, Dobrovolski et al. 2012). This study can serve as the basis for developing conservation strategies for this and other biological groups that inhabit transformed environments.

Methods

Study area

The study area is located in the central region of Sierra Madre Oriental and within the Natural Protected Area called Corredor Ecológico Sierra Madre Oriental (INEGI 2009, CONANP 2016). This area is composed of tropical forest and patches of cloud forest, being important for the species richness and their endemism. The zone is located in the eastern portion of the state of Hidalgo. Elevations range from 110 to 1700 m a. s. l; mean annual temperature is 23.7 °C and annual precipitation is 2558 mm (INEGI 2009).

Analysed environments

Surveys were carried out in tropical evergreen forest (TEF), shaded coffee plantation (SCP) and grazing area (GA) and they were identified according to the vegetation structure as described by Rzedowski (2006; Figure 1).

Tropical evergreen forest (TEF): This vegetation type shows ca. 25% of the deciduous plant species, with tree height between 20 and 30 m, with multilayer vegetation, rich in lianas and epiphytes. The herbaceous layer is composed of the species *Campelia zononia*,

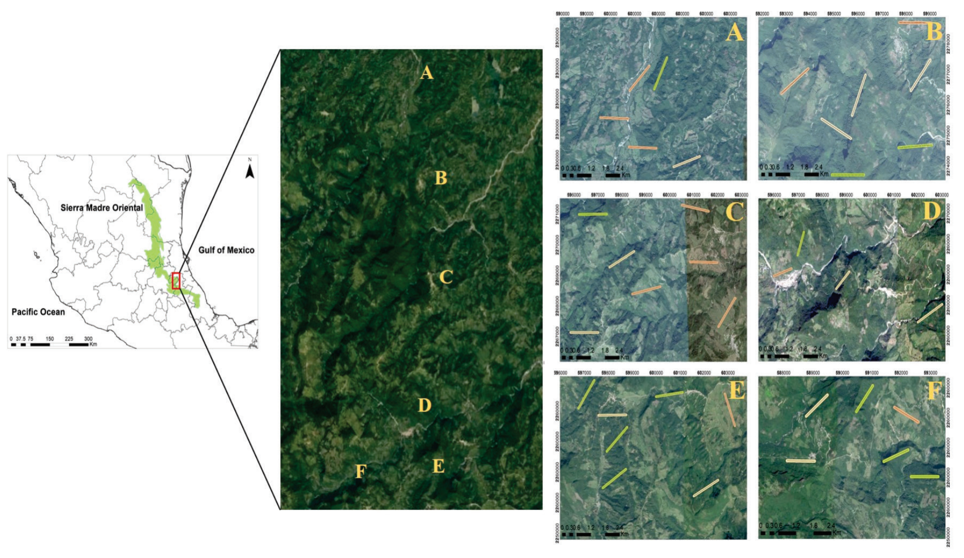

Figure 1. Location of the study area, the transects in green representing the remnants of tropical evergreen forest. Transects in brown colour show shaded coffee plantation and red transects represent grazing areas.

Fuirena simplex, *Peperomia obtusifolia* and *Zebrina pendula*; while the main arboreal species are *Cedrela odorata*, *Bursera simaruba*, *Carpodiptera ameliae*, *Persea schiedeana*, *Cecropia obtusifolia*, *Heliocarpus appendiculatus*, *Dendropanax arboreus*, *Trema micrantha* and *Jaegeria macrocephala*, amongst others (Puig 1991).

Shade coffee plantation (SCP): The SCP represents an important area of the landscape of the region (Salazar Ortiz et al. 2013). This kind of environment contributes to water retention and maintains the temperature and humidity in a manner which is not highly variable and together provides similar microhabitats to the natural forest that is used by different reptile species. Within the area of SCP, there are diverse woody plant species, such as *Alchornea latifolia*, *B. simaruba*, *C. odorata* and *Ceiba pentandra* (Salazar Ortiz et al. 2013).

Grazing area (GA): In the region, various government programmes have been developed to drive the expansion and utilisation of the grazing areas. Therefore, large areas of land of TEF have been transformed into grazing areas, which has resulted in a homogeneous environment, where the dominant grasses are *Paspalum* sp and *Andropogon* sp. (Callejas Chávez et al. 2008) and secondary vegetation formed by heliofila flora having a group succession going by herbaceous, shrubs and tree. The margins of the grazing areas are invaded by the herbaceous *Achyrates repens*, *Helenium mexicanum* and *Salvia coccinea*, while *Abutilon notolophium*, *Hamelia patens* and *Piper hispidum* are the dominant shrubs. Also, trees of the species *Acrocomia mexicana*, *Bursera simaruba*, *Parmentiera edulis*, *Ceiba pentandra* and *Tabebuia pentaphylla* together provide ecological conditions in these kinds of places (Puig 1991).

Sampling design

The fieldwork was carried out from February 2010 to January 2011, in which 12 sampling events were carried out, each with three days of surveys (one day per environment), therefore, there were 36 samplings for each environment. Due to different amounts of areas of TEF, SCP and GA, the region was subdivided into six areas of 32 km^2 each (Figure 1). Samplings were made in three different transects with a length of 1000 m × 20 m wide and each environment, independent of subdivisions, was sampled 12 times. Transects were separated by a distance of 2.5 km from each other and 12 km between areas of sampling. In each environment, three kinds of surveys were made during each visit (with three transects each), diurnal (from 09:00 h to 13:00 h), sunset (15:00 h to 19:00 h) and nocturnal (21:00 h to 01:00 h). For each environment, we invested a sampling effort of 36 person-hours (12 h × 3 persons = 36 per day), which made a total sampling effort of 1296 h for the entire study (432 person-hours per environment; Cruz-Elizalde et al. 2015).

Sampling was conducted by using direct searches for individuals in different numbers of transects per environment. Individuals were sought in different microhabitat types and habits, such as terrestrial (rocks, holes, logs), aquatic (amongst aquatic vegetation, water bodies) and arboreal (trunks, branches). The sampling period was based on the activity of the species groups. For example, lizards of the genus *Anolis* and *Ctenosaura* are diurnal and their activities peak from 0900 h to 1300 h, while *Hemidactylus*, *Lepidophyma* and the snakes *Thamnophis* and *Leptodeira* have sunset and nocturnal activity approximately from 1900 h to 2200 h (Hernández-Salinas and Ramírez-Bautista 2012).

Recorded specimens were identified in the field using dichotomous keys and released at the same place and the total number of specimens for each species was reported (Moreno 2001, Hernández-Salinas and Ramírez-Bautista 2012). The scientific names were updated following the most recent literature on the study group (Wilson et al. 2013, Meza-Lázaro and Nieto-Montes de Oca 2015).

Completeness analysis

To assess the completeness of the inventory for each environment, species accumulation curves were performed (Moreno 2001) using Bootstrap estimator, which has been considered as one of the most accurate methods to assess reptile communities more precisely, because it better highlights rare species and less so dominant species (Carvajal-Cogollo and Urbina-Cardona 2008). Likewise, algorithms that evaluate the species represented by one (singletons) or two (doubletons) individuals in the sampling were estimated (Colwell and Coddington 1994). These estimators assume that, as the sampling number increases and the curves intersect, the inventories are close to completion (Jiménez-Valverde and Hortal 2003). Species accumulation curves were performed using the programme ESTIMATES ver. 750 (Colwell and Coddington 1994).

Structure and species diversity

Rank-abundance curves were performed to assess structure and composition of the species in each community and the dominant and/or rare species for each environment were identified (Magurran 1998). On the other hand, the diversity for each community was determined with the Shannon-Wiener index using the effective number of species (Jost et al. 2010). The true diversity value was expressed as $^{I}D = \exp(H')$, where ^{I}D is the value of true diversity for each community and $\exp(H')$ is the exponential of the Shannon index (Jost 2006, Jost et al. 2010).

Results obtained from the true diversity analysis allowed the comparison of how distant the diversity is amongst communities, as well as the degree of magnitude (percentage) that distinguishes them from each other. To extract the percentage of diversity between communities we used the formula $(D_B x100)/D_A$ where D_A is the value of diversity of community A, and D_B is the value of diversity of community B (Moreno et al. 2011).

Taxonomic diversity

To assess the taxonomic diversity for each community of the environments, the taxonomic distinction of Warwick and Clarke (1995, 2001) was used, which calculates the mean (Delta = Δ^+) and the variance (Lambda = Λ^+; sensu Clarke and Warwick 1998) of the taxonomic diversity of the reptiles from each environment. This method is based on the assumption that one community with high phylogenetic relationships amongst its species will be less diverse (phylogenetically) than a community with low phylogenetic relationships amongst its species (Warwick and Clarke 1995, Clarke and Warwick 1998, Moreno et al. 2009). The formula is represented as: $\Delta^+ = [2\Sigma\Sigma_{i<j}\ \omega_{ij}]/[S\ (S-1)]$ and $\Lambda^+ = [2\Sigma\Sigma_{i<j}\ (\omega_{ij}-\Delta^+)^2]/[S\ (S-1)]$, where ω_{ij} is the taxonomic distance between each species pair j and i and S is the number of observed species in the sampling (Warwick and Clarke 1995). A high value of Δ^+ reflects a low relationship amongst species and, therefore, it is represented as a measure of taxonomic diversity. However, Λ^+ is not a measure of equity in the structure of the taxonomic diversity, thus a high value of Λ^+ indicates an under- or over- representation of the taxa in the sampling (environments).

To detect differences in the taxonomic diversity for each environment, the samples were compared (species list per environment) and the regional species pool generated a null model with 1000 re-samplings (Clarke and Warwick 1998). In this model, the average and variance of the sample numbers were used and species plotted with a confidence interval of 95% (Clarke and Warwick 1998). To assess taxonomic diversity, we used the classification by Wilson et al. (2013), which includes five taxonomic categories: species, genus, family, order and class. The analysis was developed with the PRIMER 5 programme (Clarke and Gorley 2001).

Beta diversity (β)

Finally, to determine the values of change in species composition amongst environments, we used the formula $\beta = 1\text{-}J$ (Chao et al. 2005). In this formula, J represents the values of the Jaccard similarity index that takes the values of 1 when both communities show the same species composition and 0 when the species in the communities are entirely different (Moreno 2001). This analysis was performed with PAST (Hammer et al. 2001).

Results

Species richness

In this study, 29 species of reptiles were recorded, included in 15 families and 27 genera, with the group of snakes best represented by 19 species (Table 1). Species composition was in the following order: TEF with 18 species, SCP with 13 species and GA with 12 species.

According to the species accumulation curves for each environment, in the TEF environment (Figure 2a), an asymptotic phase is shown, which indicates that the species inventory in TEF is close to being complete (95% of completeness), missing approximately only two or three species. In the SCP (Figure 2b), the same estimator showed that the species accumulation curve has not yet reached an asymptotic phase (90%); this result indicates that around four and five species remained to be recorded in this environment, even though the singletons and doubletons are crossed (Figure 2b). Finally, for GA, the estimator showed that the species inventory is complete (100%), which is consistent with the crossing of the singletons and doubletons in the species accumulation curve (Figure 2c).

Structure, composition and diversity

The abundance-rank curves showed a change in the structure of the communities inhabiting a modified environment. Structure and equity of reptile communities were similar in TEF and SCP, but distinct from GA (Figure 3). Abundance-rank curves for TEF and SCP showed that lizard species such as *Holcosus amphigrammus* and *Sceloporus variabilis* were the most dominant, while, for the GA environment, the species were *Hemidactylus frenatus* and *S. variabilis* (Figure 3). In contrast, uncommon or rare species for TEF were *Atropoides nummifer* and *Tantilla rubra*, while, for the SCP environment, *Bothrops asper* and *Micrurus diastema* were uncommon or rare. Finally, in the GA environment, *Mastigodryas melanolomus* and *Thamnophis proximus* were the rarest species (Figures 3 and 4).

On the other hand, TEF exhibited the highest value of diversity in the effective number of species with $D^1 = 14.1$, which is equivalent to the environment with greatest

Table 1. Species list and abundance of reptiles recorded during the fieldwork and in each analysed environment. TEF = tropical evergreen forest, SCP = shade coffee plantation and GA = grazing areas.

Family	Species	Acronym of species	Abundance		
			TEF	SCP	GA
Kinosternidae	*Kinosternon herrerai*	Z			8
Corytophanidae	*Basiliscus vittatus*	Ñ	2		
Dactyloidae	*Anolis naufragus*	C	8	6	
Gekkonidae	*Hemidactylus frenatus*	V			22
Iguanidae	*Ctenosaura acanthura*	Y			10
Phrynosomatidae	*Sceloporus variabilis*	B	12	8	29
Sphenomorphidae	*Scincella gemmingeri*	D	6	4	
	Scincella silvicola	H	4	5	
Teiidae	*Holcosus amphigrammus*	A	20	13	
Xantusiidae	*Lepidophyma sylvaticum*	L	3		
Boidae	*Boa imperator*	G	5		
Colubridae	*Drymarchon melanurus*	J	4	5	
	Drymobius margaritiferus	T		6	9
	Lampropeltis polyzona	I	4		
	Leptophis diplotropis	O	2	2	
	Mastigodryas melanolomus	C′			3
	Spilotes pullatus	M	3		
	Tantilla rubra	Q	2		
Dipsadidae	*Coniophanes fissidens*	E	5	2	
	Coniophanes imperialis	A′			6
	Leptodeira maculata	W			22
	Ninia diademata	F	5		
	Tropidodipsas sartorii	X			15
Elapidae	*Micrurus diastema*	N	3	2	
Natricidae	*Nerodia rhombifer*	U		4	17
	Storeria dekayi	S		6	12
	Thamnophis proximus	B′			5
Viperidae	*Atropoides nummifer*	P	2		
	Bothrops asper	K	4	1	
Totals			**94**	**64**	**158**

species richness, followed by SCP with a value of D^1 = 10.2 and GA with a similar value to the latter with D^1 = 10.1 of effective species. In this section, it is important to point out that the observed equivalences in percentage terms indicated that TEF had 28% more species than SCP and GA.

Taxonomic diversity and beta diversity

The graphs of taxonomic diversity showed that TEF and SCP present similar mean values of taxonomic diversity (58.2 and 58.5, respectively, Delta+; Figure 5a), while GA

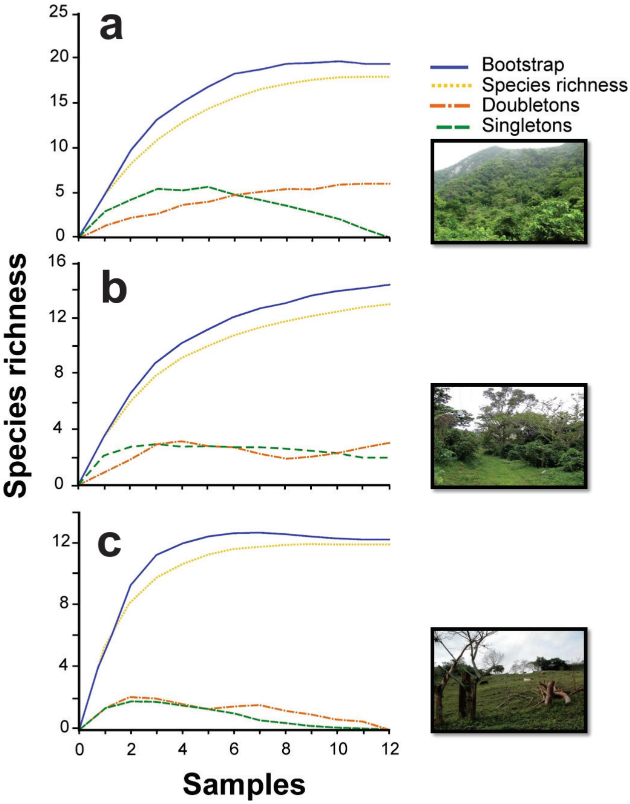

Figure 2. Species accumulation curves for **a** species of tropical evergreen forest **b** species of shaded coffee and **c** for grazing areas.

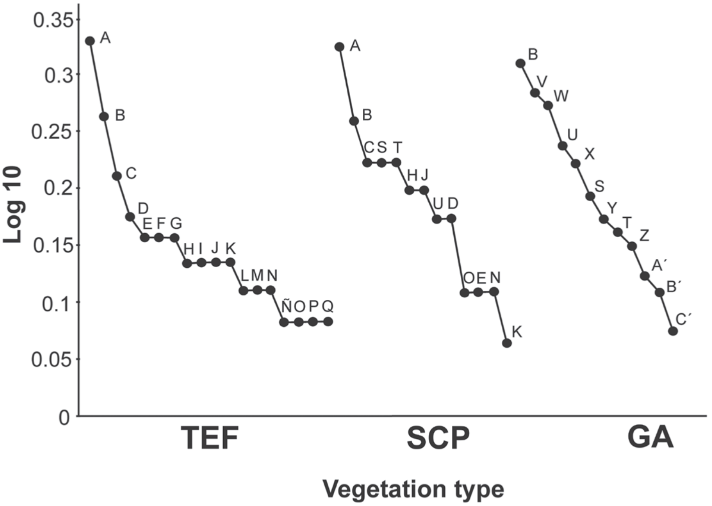

Figure 3. Curves of rank-abundance of reptiles where community composition is evaluated by type of environment. The species are represented by letters (see Table 1) in each curve (TEF = tropical evergreen forest, SCP = shaded coffee plantation and GA = grazing areas).

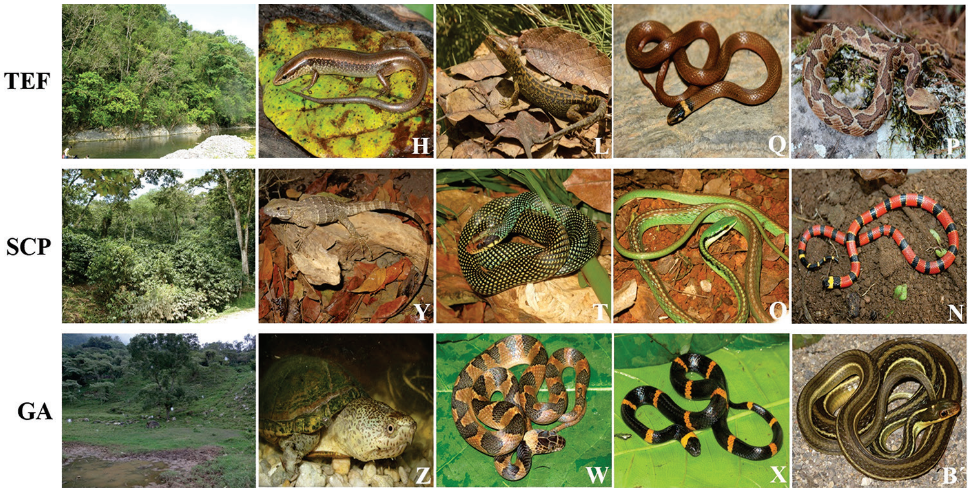

Figure 4. Reptile species that are under some risk category according to the NOM-059-2010 or whose distribution is restricted to the study region (see text). H= *Scincella silvicola*, L= *Lepidophyma sylvaticum*, Q= *Tantilla rubra*, P= *Atropoides nummifer*, Y= *Ctenosaura acanthura*, T= *Drymobius margaritiferus*, O= *Leptophis diplotropis*, N= *Micrurus diastema*, Z= *Kinosternon herrerai*, W= *Leptodeira maculata*, X= *Tropidodipsas sartorii* and B´= *Thamnophis proximus*.

showed higher values (61.2), despite having presented the lowest richness and effective number of species. The same pattern occurred in the variation of taxonomic diversity, where TEF and SCP showed similar values (38.5 and 38.7, respectively), while the greatest value for GA was 107.6 (Lambda+; Figure 5b). Finally, with respect to beta diversity, the values were elevated between TEF and GA with 0.97 and between SCP and GA with 0.81; the lowest value was between TEF and SCP with 0.52.

Discussion

The richness, diversity and composition of reptile species in the analysed environments were different from each other. The results showed a general pattern of species loss and change in structure communities from preserved forest remnants to areas of SCP and GA. This pattern could be driven by the loss of vegetation cover, as well as loss of water bodies and changes in humidity and temperature amongst places, which together provide appropriate conditions (e.g. ideal microhabitats) to be exploited by different species of reptiles (Gardner et al. 2007). Therefore, habitat transformation directly influences species richness and its abundance. Malcolm (1994) found similar results when he analysed the richness and species diversity from different biological groups in fragmented forests from Brazil. This pattern of change of species amongst environments has also been observed in other studies. For example, Philpott et al. (2008) found that there is a significant loss of ants, birds and trees in coffee systems. These authors have argued that the anthropogenic factors, such as construction of communication routes,

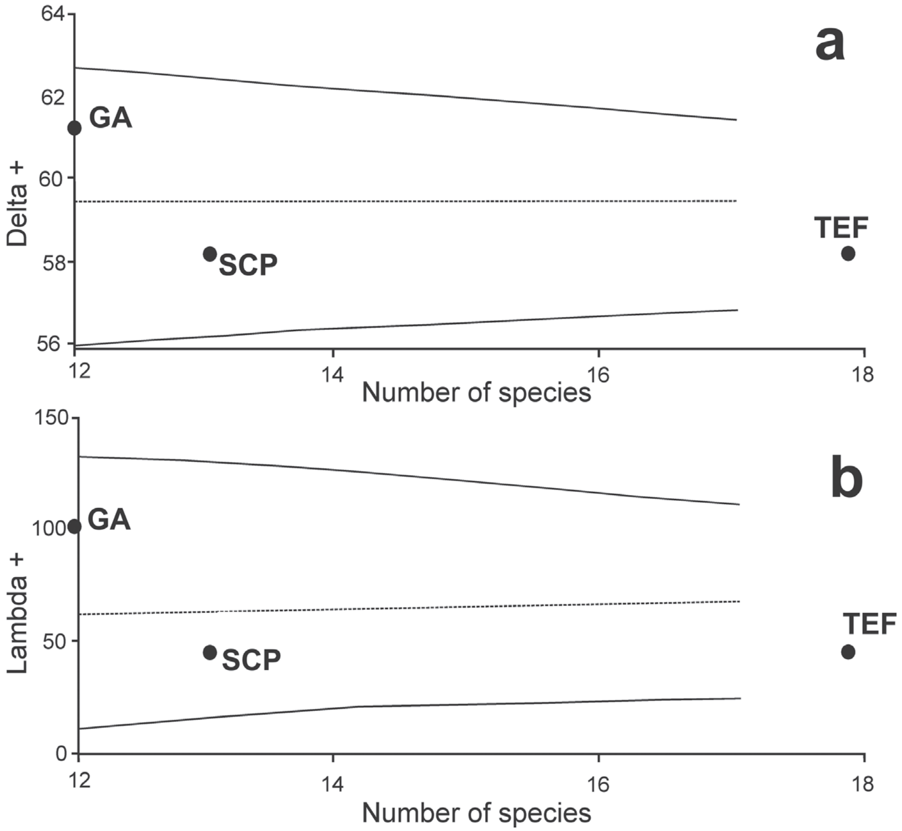

Figure 5. Average of taxonomic diversity (a; Delta+) and variation in taxonomic diversity (b; Lambda+) for the analysed environments (TEF, SCP and GA). Continuous lines represent confidence interval at 95% according to the null model.

home constructions and deforestation for grazing areas negatively affect reptile species distribution at the local level (Dornelas et al. 2011).

Analysis of completeness indicated that there are still species to record in SCP and TEF, while GA showed the highest percentage of completeness. This pattern might be caused by two factors, *i*) the method used in this study and *ii*) the complex structure pertaining to each environment. GA showed a low number of microhabitat types which could be occupied by reptile species, including rocky crevices, logs, hollows of trees or water bodies. While the opposite was observed in SCP and TEF, with both sites containing leaf litter, logs, bromeliads and undergrowth at the edge of water bodies. Therefore, heterogeneity in microhabitats tends to make it more difficult to observe all individuals belonging to each species (Vitt et al. 2007).

Tropical evergreen forest showed the greatest species richness, as well as a high number of exclusive species. These species are represented with low abundance, mainly in the snakes *A. nummifer*, *Boa imperator*, *Ninia diademata* and *T. rubra*; in contrast, GA had less species richness but showed a high abundance, for example, in *H. frenatus*, *N. rhombifer*, *S. variabilis* and *L. maculata* (Table 1). SCP did not contain exclusive species; however, in this environment, the species *H. amphigrammus* and *Scincella gemmingeri* occurred with high abundance (Table 1). These results are similar to other studies that compare species composition amongst environments with different vegetation structure; for example, Pianka (1989) and Urbina-Cardona et al. (2006) found that lizard species, which prefer open areas, showed higher population sizes than populations inhabiting preserved forests (Gardner et al. 2007). In our study, *S. variabilis*, *H. frenatus* and *Ctenosaura acanthura* were found in high abundance in open areas of GA. The permanence of the species in each environment is influenced by their generalist habits and use of the different microhabitat types in the modified environment. SCP showed microhabitat conditions of temperature and humidity that promote the establishment of some reptile species, such as those which occurred in this study.

With regards to the equity, this is a measure of species diversity considered in studies on structure and species composition of an environment (see Magurran and McGill 2011). This measure allowed the determination that GA differed highly from TEF and SCP in number and abundance of species. This pattern was due to a greater species number, including *inter alia*, *H. frenatus*, *S. variabilis* and *Storeria dekayi*, which are considered tolerant to those conditions found in homogeneous environments such as GA and because these species have been reported as abundant (Martín-Regalado et al. 2011).

The results of diversity and composition of communities of reptiles in each environment are supported by a taxonomic diversity analysis (a measure complementary to species diversity), where TEF and SCP were similar in this value of diversity; however, GA showed higher values (Figure 5a). These values of taxonomic diversity between TEF and SCP exhibited a high similarity in composition of species, genera and families; therefore, it suggests a similar sensitivity to the modification of the TEF and SCP environments, as was observed by Wanger et al. (2010). These authors compared the richness and diversity of amphibians and reptiles amongst environments with different degrees of disturbance and recognised that amphibians were more abundant in disturbed than conserved environments; consequently, disturbed habitats had high values of diversity. GA showed the highest value of taxonomic diversity and, in this site, *Kinosternon herrerai*, *L. maculata* and *S. variabilis* were present. These species are characterised by high displacement and tolerance to modified environments, in contrast to those species that occurred in TEF and SCP, with which it showed the highest values of beta diversity (0.97 and 0.81, respectively). These differences in species number and composition of communities of reptiles show a reduction in diversity from small portions of tropical forest to areas under agricultural management (Luja Molina 2005). Our study showed a similar pattern, in which TEF and SCP lost 72% of the reptile diversity when they are transformed to GA.

In summary, a change in species number from TEF to SCP and GA showed a pattern of species loss. From TEF to SCP, there was species loss while, from TEF to GA, there was severe loss and replacement by new, supposedly opportunistic species. TEF and SCP, however, maintained a similar diversity and species composition of reptiles, indicating that transformed environments with similar characteristics to the untransformed forest contribute to the persistence of species richness. Therefore, in addition to the analysis of richness, diversity and structure of the reptile communities amongst environments, the size of the patches, edge effect and the surrounding matrix of the fragments of the untransformed forest should also be analysed in order to identify the consequences of these factors on maintenance or loss of species. The assessment of these variables (factors) will allow the recognition of more efficient spatial turnovers. Additionally, maintenance or loss of species amongst environments might change according to the availability of resources (space-food), which in turn are influenced by environmental factors, such as temperature, precipitation and humidity (Vitt and Caldwell 2009).

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First record of the protected species *Pinna nobilis* (Linnaeus, 1758) in the Aquatina Lagoon (NATURA 2000 site IT9150003, South-East Italian coastline)

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Abstract
Information on the presence of *Pinna nobilis* (Linnaeus, 1758) in the Mediterranean Sea is largely reported in literature because it is an endemic and, at the same time, endangered species. Besides, this record contributes to enlarge the spatial distribution of this species in the South-East Italian coastline (Adriatic Sea). *P. nobilis* is a protected species under the EU Habitats Directive (1992). In particular, *P. nobilis* has been recorded for the first time in the Aquatina Lagoon, a transitional water ecosystem included in the NATURA 2000 site "*Aquatina di Frigole*" (IT9150003). Therefore, this finding underlines the role of transitional water ecosystems as "nursery habitats" for *P. nobilis* as well as the relevance of conservation actions introduced by the EU with the NATURA 2000 network for preserving the biodiversity.

Keywords
pen shell, *Pinna nobilis*, transitional water ecosystems, NATURA 2000 network

Introduction

The key species *Pinna nobilis* Linnaeus, 1758, also called pen/fan shell, is an endemic species identified in the Mediterranean Sea since the Miocene Era (Gómez-Alba 1988). It is the largest bivalve mollusc in the Mediterranean Sea, exceeding one metre in total length (García-March and Vincente 2006), living up to 27 years (García-March et al. 2008) at depths ranging from 0.5 to 60 m (Butler et al. 1993). Its main habitat is marine soft-bottom, with the presence of seagrass meadows of *Posidonia oceanica* (L.) Delile 1813 and/or *Cymodocea nodosa* (Ucria) Asch. 1870 (Zavodnik, Hrs-Brenko & Legac 1991). Besides, it was also recognised in unvegetated estuarine areas (Addis et al. 2009) and unvegetated soft bottoms of marine areas (Katsanevakis 2005). Regarding its ecological role, *P. nobilis* is a "filter feeder species" and its surfaces are usually colonised by other benthic species, including algae and macroinvertebrates, thus increasing the local biodiversity. For these reasons, *P. nobilis* supplies many ecosystem services by retaining a large amount of organic matter from suspended detritus (e.g. water clarity), hosting other species (e.g. biodiversity) and attracting scuba-divers (e.g. tourism and recreation). From the time of the Egyptians and Romans, this species has been considered a marine resource for human exploitation due to the high-value of handmade cloth obtained from the byssus, the so-called "sea silk" and as a food source in some Mediterranean regions by traditional uses and cooking (Katsanevakis et al. 2011). Nowadays, *P. nobilis* is a protected species under the EU Habitats Directive (1992), Bern Convention and Barcelona Convention Protocol (Annex II). For its ecological relevance, currently the pen shell is a target species for assessing the descriptor 1 "*Biological diversity*" and 4 "*Status of the single structural components of ecosystems*" of the "Marine Strategy Framework Directive (MSFD 56/EC, 2008)" of the European Union to be applied practically to achieve Good Environmental Status (GES) by 2020.

Despite its ecological relevance, the conservation actions and the current interest as a target species in the MSFD, *P. nobilis* is highly vulnerable to illegal exploitation and it is threatened by abiotic and biotic sources of perturbations (e.g. climate change, parasites). For all the above reasons, a more detailed description of the occurrence of *P. nobilis* in the Mediterranean Ecoregion is required to preserve this species.

Here, we describe the first record of *P. nobilis* in a transitional water ecosystem located in Italy along the coastline of the South Adriatic Sea (Aquatina Lagoon) and included in a NATURA 2000 site. In this lagoon, the presence of *P. nobilis* has never been previously recorded. This finding suggests that Mediterranean coastal lagoons could be considered as "nursery ecosystems" for the recruitment of the species as well as for other marine species and underlines the effectiveness of the NATAURA 2000 network for preserving the biodiversity.

Materials and methods

The high relevance of this first record is due to the fact that the species *P. nobilis* has been recognised in a transitional water ecosystem, Aquatina Lagoon (40.442463°N – 18.237675°E; Fig. 1), included in the NATURA 2000 site named "*Aquatina di Frigole*" (IT9150003).

At the beginning of January 2018 and during an exceptional low tide, we observed some specimens of *P. nobilis* had partially emerged. After this finding, we conducted

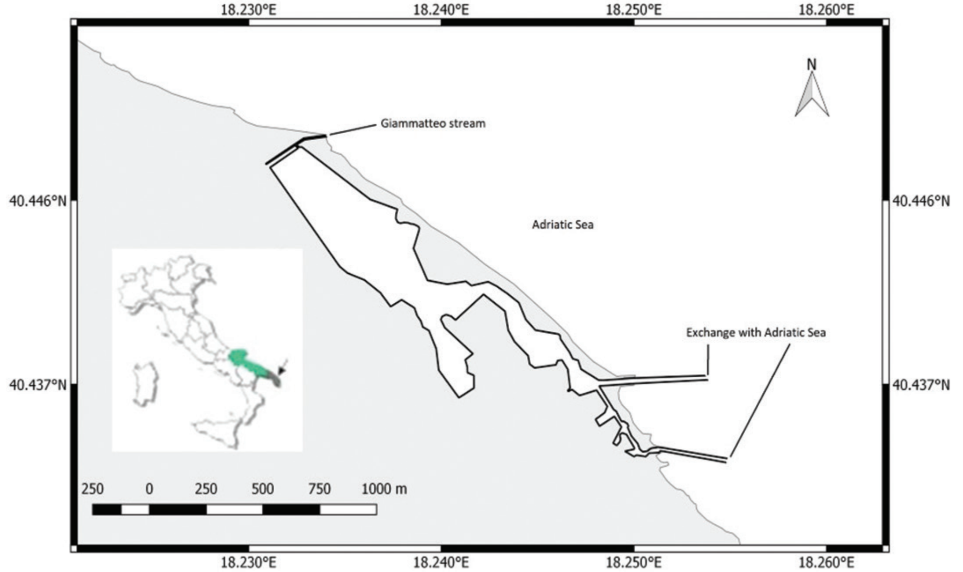

Figure 1. Location and map of Aquatina Lagoon (South-East Italian coastline). The lagoon is included in the NATURA 2000 site "*Aquatina di Frigole*" - IT9150003.

in the area close to the lagoon mouth an underwater *visual census* (Fig. 2) along 3 transects of 20 m length and 2 m width in order to survey and count the fan mussel *P. nobilis* specimens, to estimate the population density and to monitor the individual vitality and size, measured according to García-March and Vicente (2006). Sampling was carried out during the first week of February 2018 in the Aquatina Lagoon. The lagoon's surface is 42 hectares, representing about 3% of the whole NATURA 2000 site "*Aquatina di Frigole*" (IT9150003). Its maximum depth is approx. 1.5 m, while its maximum tidal excursion, on an annual basis, is approximately 34 cm (Petrocelli et al. 2009). It is linked to the nearby sea by a channel 15 m wide and 400 m long. The Aquatina Lagoon is characterised by a superficial saltwater-bearing stratum and a relatively low depth. The sediments of the lagoon are colonised by *Cymodocea nodosa* and *Posidonia oceanica* debris. Aquatina is a shallow water body, so that decomposition and biogeochemical processes in the lagoon sediment interfere strongly with the nutrient dynamics in the water column. In the wet season, the phytoplankton community (Giacobbe et al. 1996) is principally constituted by nanoplanktonic taxa (*Cyanophycees* and *Phytoflagellates*), while in the dry season, the phytoplankton community is dominated by the microplankton fraction, *Navicula* spp., *Cylindrotheca closterium*, *Prorocentrum micans* and *Prorocentrum minimum*. Improving water exchange with the sea is leading to an increase in marine species in the lagoon which are substituting the freshwater species (Cappello et al. 2005).

The study of population structure of *P. nobilis* shows an instantaneous image and provides a quantitative approximation of the stock of the population. The possibility

Figure 2. A specimen of *Pinna nobilis* in the Aquatina Lagoon (NATURA 2000 site "*Aquatina di Frigole*" IT9150003).

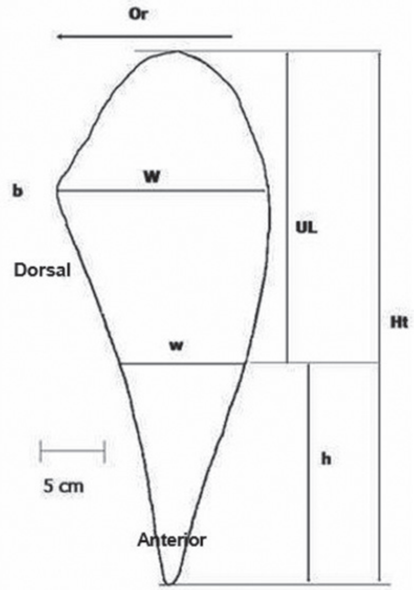

Figure 3. Measurements of interest to estimate the orientation and body-size of *Pinna nobilis*. *In situ* can be measured: W and w, maximum and minimum width respectively; UL, unburied length and Or, orientation of the gape. Maximum shell length (Ht) and length of the buried part (h) can be measured by removing the specimens from the bottom. Besides, Ht can be estimated by applying specific mathematical models (Garcia-March and Vicente 2006).

Figure 4. Biometric measurements of *Pinna nobilis*. Due to an exceptional low-tide day, some specimens were partially emerged.

and benefits of carrying out an explorative sampling should always be the first aspect to be considered when a field survey to study *P. nobilis* populations is going to be undertaken. This is the cheapest and fastest option, but also that in which the least information is compiled. Data gathered is qualitative or the counts of individuals are inaccurate and not referred to a surface area and few statistics -if any- are required to analyse the results. The specimens found were measured according to the protocol proposed by García-March and Vicente (2006) (Fig. 3). In situ, for all recorded animals, the unburied length (UL), maximum width (W) and minimum width (w) were measured by a measuring-tape (Fig. 4). The estimation of maximum antero-posterior shell length of *P. nobilis* cannot be made directly because individuals do not withstand the shedding of the byssus when unburied. Consequently, maximum shell length (Ht) must be estimated indirectly, using empirical equations to relate the measurements of unburied shell parts with Ht. The total height of the fan shell was estimated by using the equation: $Ht = UL+(1.79w + 0.5)$ according to Garcia-March et al. (2002) and Garcia-March and Vicente (2006). Three measurements are basic for estimating Ht, i.e. maximum and minimum width (W and w) and unburied length (UL). Gape orientation (Or) was measured by a compass. This is important from an ecological point of view because orientation of the gape indicates the position of maximum drag force

(Fd) supported by the shell and also in determining the composition of the epibiontic community living on the shell. It is measured with respect to the bend of the shell (dorsal part). For convenience, the bend /dorsal part are always at the opposite side where the orientation is measured. Finally, temperature, dissolved oxygen, salinity and the pH of the water column were measured and recorded by means of a hand-held multiprobe (YSI 556 - YSI Inc., Yellow Springs, OH).

Results

Eleven specimens of *P. nobilis* were recorded; they were orientated in the North-East direction, ranging from 5° to 80° NNE. Maximum and minimum widths were 15.16 cm ± 0.726 and 13.81 cm ± 0.611, respectively and the unburied length was 16.66 cm ± 0.441. The abiotic parameters of water column were also recorded (temperature 12.69°C ± 0.207, dissolved oxygen 7.21 $mg*l^{-1}$ ± 0.278, salinity 24.77 PSU ± 0.963, pH 7.73 ± 0.084).

Discussion

Probably the presence of *P. nobilis* in the Aquatina Lagoon is relatively recent because the species was not recorded in the last update of NATURA 2000 Standard Data Forms (2015). This finding can be justified by the availability of food which seems to be a driving force in determining the patchy distribution of *P. nobilis* populations. In marine habitats, the fan mussel seems to favour meadows of the marine seagrass with *P. oceanica* and *C. nodosa* (Zavodnik et al., 1991) and its distribution is strictly overlapped with the presence of *P. oceanica* meadows (Richardson et al. 1999). Coppa et al. (2013) stated that a higher efficiency in the filtering activity of *P. nobilis* on the meadow borders is related to a satisfactory hydrodynamic for efficient filtering action, explaining the specimen aggregation on the edges. In contrast, within the meadow where the water flow is reduced by seagrass leaves (Koch et al. 2006, Manca 2010), the efficiency of filtering activity of the fan shells could be reduced. In general, the distribution of all benthic macroinvertebrate species is related to bottom habitat types (Galuppo et al. 2007).

In the Aquatina Lagoon, the relative position of the specimens in relation to the meadows was not studied because only dead leaves of *P. oceanica* were present in the lagoon bottom. Besides, the presence of *P. nobilis* in the proximity of the lagoon mouth could be justified by a constant hydro-dynamism and water exchanges with the sea and the recruitment of juveniles from the sea. Since *P. nobilis* is actually exposed to many abiotic and biotic sources of perturbations that are dramatically depleting the populations in the Mediterranean Sea (Vázquez-Luis et al. 2017), this new record becomes significantly relevant in confirming the presence of a new population in the Adriatic Sea. Actually, the ecological assessment of lagoons, traditionally done by the sampling of the benthic macroinvertebrate communities (Evagelopoulos et al. 2008; Pinna et al. 2013), requires the application of time-consuming and high cost procedures; on the contrary, the monitoring of *P. nobilis*, the largest body-size benthic macroinvertebrate species of the Mediterranean Sea, is faster and cheaper and could suggest the developing of new and smart ecological indicators for rapid assessment of Mediterranean lagoons, as well as for innovative eco-genomic tools (Pawlowski et al. 2018). The results of our research show the relevance of the NATURA 2000 network as an effective tool for biodiversity conservation at EU scale and, moreover, underline the importance of Mediterranean transitional water ecosystems as "nursery habitat" for *P. nobilis* as well as their potential use for promoting breeding programmes in the Aquatina Lagoon and future restocking of resistant juvenile individuals. Until now, the interest in the monitoring of *P. nobilis* is focused only on marine ecosystems but we hope that the monitoring programmes for *P. nobilis* in EU countries will also be extended to transitional aquatic ecosystems as soon as possible.

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RESEARCH ARTICLE

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Applying bayesian population assessment models to artisanal, multispecies fisheries in the Northern Mokran Sea, Iran

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Abstract

Small-scale fisheries substantially contribute to the reduction of poverty, local economies and food safety in many countries. However, limited and low-quality catches and effort data for small-scale fisheries complicate the stock assessment and management. Bayesian modelling has been advocated when assessing fisheries with limited data. Specifically, Bayesian models can incorporate information of the multiple sources, improve precision in the stock assessments and provide specific levels of uncertainty for estimating the relevant parameters. In this study, therefore, the state-space Bayesian generalised surplus production models will be used in order to estimate the stock status of fourteen Demersal fish species targeted by small-scale fisheries in Sistan and Baluchestan, Iran. The model was estimated using Markov chain Monte Carlo (MCMC) and Gibbs Sampling. Model parameter estimates were evaluated by the formal convergence and stationarity diagnostic tests, indicating convergence and accuracy. They were also aligned with existing parameter estimates for fourteen species of the other locations. This suggests model reliability and demonstrates the utility of Bayesian models. According to estimated fisheries' management reference points, all assessed fish stocks appear to be overfished. Overfishing considered, the current fisheries management strategies for the small-scale fisheries may need some adjustments to warrant the long-term viability of the fisheries.

Keywords

Small-scale Demersal fisheries, Bayesian modelling, Generalised surplus production

Introduction

Human dependency on maritime and coastal resources is increasing (Berkes 2001). It is often indicated that a small-scale fishery is a mainly pro-poor activity because it is an economic sector that is labour-intensive and comparatively easy to enter; and provides the fields of livings to a large number of uneducated people, including women through their participation in fish processing activities. These small-scale artisanal fisheries substantially contribute to the poverty alleviation, local economies and food security in many countries. They engage 50 of the world's 51 million fishermen, all of whom are actually from developing countries (Neiland and Béné 2013). In the tropical and subtropical coastal domains, small-scale fisheries account for the majority of catches (Berkes 2001; Salas et al. 2007) and are considered as the more sustainable method of fishing (Matthew 2003; Pauly 2006).

Increased over-exploitation of fishery and habitat destruction threaten the coastal and maritime resources. Small-scale fisheries often have limited and low-quality catch and effort data that complicates stock assessment and management. Globally, for example, only 10% to 50% of fish stocks in more developed countries and 5% to 20% of fish stocks in less-developed countries have been scientifically assessed due to limited data (Chen et al. 2003; Costello et al. 2012; Jiao et al. 2011). To enhance the sustainability of small-scale fisheries, therefore, suitable and reliable stock assessments are required (Berkes 2001; Hilborn and Walters 1992; Jiao et al. 2011; Xiao 1998).

Based on the various works (Valinassab et al. 2010; Valinassab et al. 2003; Valinassab et al. 2006; Valinassab et al. 2005) and the reports from the Offshore Fisheries Research Centre of Chabahar (OFRC) and the Provincial Fisheries Department of Sistan and Balochestan (PFDSB), the following fourteen demersal fish species are the most important economically: Fourfinger threadfin (*Elutheronema tetradactylum*), Smalltooth emperors (*Lethrinus microdon*), John's snapper (*Lutjanus johni*), Malabar blood snapper (*Lutjanus malabaricus*), Tigertooth croaker (*Otolithes ruber*), Silver pomfret (*Pampus argenteus*), Black pomfret (*Parastromateus niger*), Bartail flathead (*Platycephalus indicus*), Javelin grunter (*Pomadasys kaakan*), Blackspotted croaker (*Protonibea diacanthus*), Greater lizardfish (*Saurida tumbil*), Talang queen fish (*Scomberoides* commersonnianus), Goldlined seabream (*Rhabdosargus sarba*) and Indian pompano (*Trachinotus mookalee*). In addition, the above-mentioned fish species have been recorded as the kinds that their abundance is in reduction and local extinctions have been recorded by relevant organisations such as Iran Fisheries Organization (IFO) and PFDSB. However, no wide fishery stock assessments have been undertaken. Therefore, they are selected as targeted species in current study.

Mostly, due to insufficient information about the time series of biological and management reference points of fish stocks, the scientific precise stock assessments have not been undertaken for the majority of fish species in Iran, especially in the southern coastal areas (the current study area). Therefore, due to the lack of information toward fisheries management reference points, most fisheries planning has not had any special effects on the sustainability of fish stocks reserves.

So far, there has been a lot of scientific motivation for assessing fish stocks in Iran, but it has not been implemented for two reasons; one the lack of sufficient information used in scientific stock assessment methods and second the complexity and time-consuming of stock assessment methods in the limited-data situations.

Bayesian modelling has been advocated to assess fisheries with limited data. Specifically, Bayesian models can incorporate information of the multiple sources such as academic literature, empirical research, biological theory and specialist judgement. This characteristic of the Bayesian models improves precision in the stock assessments and provides the specific levels of uncertainty for estimating the parameters (Kuparinen et al. 2012; McAllister and Kirkwood 1998; Punt et al. 2011).

Therefore, in the current study, because of the limited data, the state-space Bayesian generalised surplus production models used to estimate the stocks status of the fourteen demersal fish species targeted by small-scale fisheries in Sistan and Baluchestan (A coastal province south-east of Iran). This could provide scientific knowledge for the fisheries management and contribute to the researchers applying and improving the results of the current study in order to achieve the global environmental sustainability and marine ecology.

Hence, in the current study, based on the above-mentioned stock assessment Bayesian approach, the management reference points provided for the fourteen fish species, including biomass, harvest rate and stock status, the implication of these for the sustainable management of the small-scale fisheries was discussed. Moreover, the estimates of biological parameters were compared to the previous findings of the fourteen species.

Materials, methods and data selection

Study area and data source

The fisheries examined in this study are located in the Sistan and Baluchestan Province (SBP) situated at the northern end of Mokran Sea (Gulf of Oman) in Iran (Pakzad et al. 2014). There are ten ports along a 270 km (167.77 miles) stretch of coastline from Govater Bay in the East to Kereti Bay in the West, spanning a longitude 59°13'E to 61°13'E (Figure 1).

Based on the local reportage of PFDSB and IFO, the fishery is an important source of income, cultural heritage and recreation in the area. In addition, it forms the largest employment with over 24,500 locals involved in fishing industries permanently or seasonally. The fishing system of SBP consists of inshore fleets, with 60% (1430) of vessels registered as weighing at least three gross tonnes, as most of which are primarily made of fibreglass. The fishing activities are mainly seasonal and fishermen change their fishing gear (gill nets, hand-lines/hook-and-lines and traps) and strategies based on water levels, habitats, migration patterns and species targeted. However, the majority of vessels that fish annually use gill nets. The total catches of

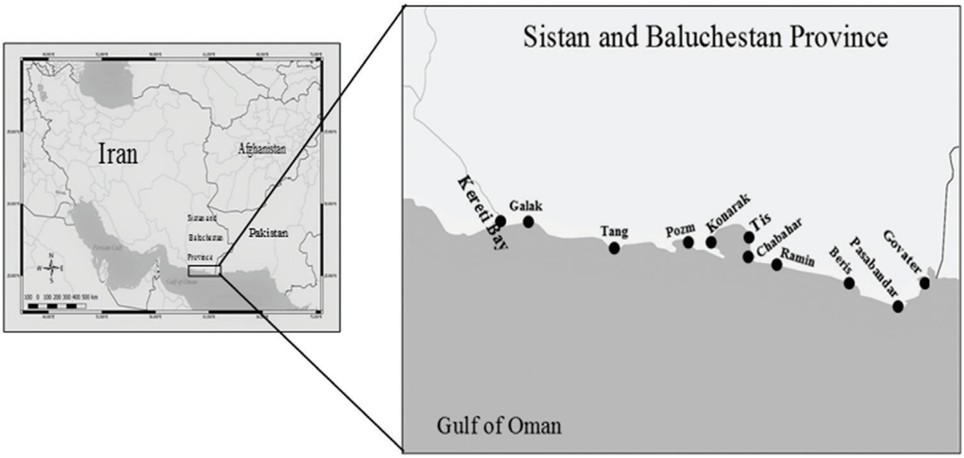


Figure 1. Study area and the locations of fishing landing ports related to small scale fishing vessels.

the fourteen species examined in this study from 21 March 2015 to 18 March 2016 were 35,937 metric tonnes. This catch comprises 49% of the demersal fish catch; 31% of all fish species caught and 187 million US$ of economic value which represents an important resource for the fishery.

Nine years (21 March 2006 to 18 March 2015) of fisheries-dependent commercial landings and effort data for the fourteen demersal fish species listed earlier were acquired from Iran's National Fishery Data Collection and Reporting System Unit and also reports from the Provincial Fisheries Department. In addition, the used time series of catch and standardised CPUE values as relative abundance indices are considerable as the supplementary data. The nominal CPUE indices that derived from commercial fisheries' logbooks are affected by some variables such as spatiotemporal and environmental factors. The considered standardised CPUE indices are reliable abundance indices which allow the implementation of the conservation and management measures and have been obtained by the most common and competent statistical approach in the domain of fisheries' researches, such as generalised additive models (GAMs), that are used for standardising catch and effort data.

Modelling methods

Biomass dynamic models are popularly used for stock assessment when only catch and effort time series data are accessible (Hilborn and Walters 1992; Kinas 1996; Laloë 1995; Mäntyniemi et al. 2015; Quinn and Deriso 1999). These models equate current biomass as previous biomass plus surplus production (growth, recruitment and natural mortality) minus harvest removals (Hilborn and Walters 1992; McAllister and Kirkwood 1998; Schaefer 1957).

The biomass dynamics model of the equation discrete time form is as follows (Hilborn and Walters 1992):

$$B_t = B_{t-1} + h(B_{t-1}) - C_{t-1} \tag{1}$$

In Equation 1, B_{t-1}, C_{t-} and $h(B_{t-1})$ denote biomass and catch for year t–1 and the surplus production function, respectively.

Bayesian state-space surplus production model

Bayesian state-space models consist of three levels (Berliner 1996; De Valpine and Hastings 2002; Haddon 2010; Parent and Rivot 2012) as follows:

(I) a process equation which depicts the time dynamics of a stochastic process as a function of time-invariant hyper-parameters. (II) an observation equation based on population-specific inspection data that are a function of the unobserved state process (Buckland et al. 2004). (III) the prior distributions level that comprises an explanation of the prior probability distribution of the parameters and condition at the first time moment (Rankin and Lemos 2015). These three levels are specified in the following section in the background of a surplus production model.

Process equation

With regards to the Equation 1, the process equation describes the surplus production function in a generalised surplus production model (GSPM) (Fletcher 1978; Pella and Tomlinson 1969) as follows:

$$h(B_{t-1}) = r\,B_{t-1}(1 - (B_{t-1} / K)^z),\ r > 0,\ K > 0,\ z > 0 \tag{2}$$

where r is the intrinsic population growth rate; K is the carrying capacity of the population and z is the shape parameter of the production model that determines at which B/K ratio maximum surplus production was attained and commonly noted as equivalent biomass and at which the maximum sustainable yield (MSY) was attained (B_{MSY}). If the shape parameter was less than unity ($0 < z < 1$), then surplus production would increase (to the peak point) when the biomass was below K/2 (a left-skewed production curve). If the shape parameter was greater than unity ($z > 1$), then biomass production would increase (to the peak point) when the biomass was more than K/2 (a right-skewed production curve). If the shape parameter was identical to unity ($z = 1$), the production model would reduce to the Schafer form, attaining MSY when biomass was equal to K/2. If z approached zero ($z \rightarrow 0$), the production model would reduce to the Fox model that results into maximum surplus production at ~0.37K.

Replacing Equation 2 in Equation 1 and multiplying the right hand side of the resultant equation with u_t yields the stochastic form of the biomass dynamic model with generalised surplus production (GSP) (Parent and Rivot 2012):

$$B_t = (B_{t-1} + r_t B_{t-1}(1 - (B_{t-1} / K)^z) - C_{t-1})u_t \tag{3}$$

Where u_t is process noise – supposed to be independent and log-normally distributed; specifically $u_t = e^{\varepsilon_t}$ where $\varepsilon_t \sim N[0, \sigma^2]$, *i.e.* ε_t is i.i.d. normal with mean zero and variance σ^2.

Equation 3 was re-parameterised using relative biomass ($P = B_t / K$) to diminish parameter confounding such as that between biomass and K that could result in related priors (Meyer and Millar 1999) as follows. Thus, the final stochastic form of the process equation is given by Equation 4:

$$P_t = (P_{t-1} + \mathrm{r}_t P_{t-1}(1 - (P_{t-1})^z) - C_{t-1} / K)u_t \tag{4}$$

Observation equation

According to regular assumptions, CPUE values are relative abundance indices proportional to the biomass. The observation equation relates the unobserved states B_t to the relative abundance indices I_t (Harley et al. 2001; Bishop 2006; Ye and Dennis 2009; Yu et al. 2013). Thus, the observation equation with log-normally distributed errors to attain the stochastic observation equation (Rankin and Lemos 2015) can be written as Equation 5:

$$I_t = qKP_t \upsilon_t \tag{5}$$

where I_t is the relative biomass index; q is the "catchability" coefficient that indicates the effectiveness of each unit of fishing effort and υ_t is the observation error entered as an independent and log-normally distributed random variable. Specifically, $\upsilon_t = \mathrm{e}^{\eta_t}$ where $\eta_t \sim N[0, \tau^2]$, *i.e.* is η_t i.i.d. normal with mean zero and variance τ^2.

Parameter prior distribution layer

An advantage of the Bayesian models is its ability to use the prior distributions based upon the existing knowledge to set plausible values for model parameters (Gelman et al. 2014). The generalised surplus production model (GSPM) parameters include the carrying capacity K, the intrinsic growth rate r, the shape parameter z, the catchability coefficient q, the process and observation noise variances σ^2 and τ^2 and the proportion of initial biomass to carrying capacity P.

The reason for choosing the priors was based on the following rationale. First, based on the expert consultations of IFO and PFDSB and the available information from Valinassab et al. 2010; Valinassab et al. 2003; Valinassab et al. 2006 and Valinassab et al. 2005, an objective and informative uniform prior for carrying capacity, K, was specified with a lower frontier of the supreme reported landings and an upper frontier equal to fifty times the lower boundary as values below or above this are unlikely. According to Cheung and Sumaila (2015), FishBase (http://www.fishbase.org), and expert consultations of OFRC and PFDSB, an objective and informative lognormal distribution priors were adopted for the intrinsic growth rate *r*. Based on the method presented in Parent and Rivot (2012) and Montenegro and Branco (2016), a rather diffuse prior (inverse-Gamma (0.001,0.001)) provided for the catchability coefficient *q,* and also, according to King et al. 2009, a non-informative gamma distribution prior with parameters (2,2), selected for the shape parameter *z*. In addition, the considerable prior in Table 1 for the initial relative biomass P[1], was based on Valinassab et al. 2010; Valinassab et al. 2003; Valinassab et al. 2006; and Valinassab et al. 2005 and reported landings from IFO and PFDSB were specified as an objective and informative lognormal distribution. In addition, some required procedure of the used prior distributions functions were presented in (Appendix 1) for parameters.

Based on Kéry and Schaub (2011) and Gelman and Meng (2004), Jiao et al. (2008), Meyer and Millar (1999), Millar (2002), and Seaman et al. (2012), the Bayesian population assessments, particularly estimates of state-space models, especially the process and observation noise variances σ^2 and τ^2, are more sensitive to the prior specifications than the other parameters. Therefore, in order to ensure that the results of the study were not misleading due to the inappropriate selection of prior distribution of the σ^2 and τ^2, the various prior distribution combinations were opted and examined as follows. In the first stage, the same Inverse-Gamma with parameters (0.001, 0.001) was designated for the above-mentioned two variance parameters. With those priors, the Markov Chain Monte Carlo (MCMC) algorithm convergence and stationarity were not verified based on the formal diagnosis tests. Therefore, a uniform prior distribution U (0, 100) was used for the σ^2 and τ^2, equivalently. Again, as in the previous stage, the (MCMC) algorithm convergence and stationarity were not confirmed based on formal diagnosis tests. Finally, after a trial and error process on changing the shape and scale parameters of Inverse-Gamma distribution, the best prior distribution as two Inverse-Gamma with parameters (15, 0.1) and (10, 0.1) was selected for the process and observation noise variances σ^2 and τ^2, respectively. Furthermore, to the aforementioned prior distributions details, a summary of the prior distribution values for the P [1], K and r is presented in Table 1.

Fisheries management reference points

The major fisheries reference points for the GSPM (Chaloupka and Balazs 2007; Punt and Szuwalski 2012; Zhu et al. 2014) examined in this study are as follows:

Table 1. Summary of the Prior distribution functions used for some parameters of all bayesian state-space GSPM Fourteen specified high-commercial demersal fish species.

Species	Parameter		
	Intrinsic growth rate, r	**Carrying capacity, K**	**Initial condition, P[1]**
Elutheronema tetradactylum	r ~ lognormal(-1.1139,4.4814)	K ~ uniform(604,30200)	pi ~ uniform(0.01,0.135) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)
Lethrinus microdon	r ~ lognormal(-0.2326,4.4814)	K ~ uniform(1089,54450)	pi ~ uniform(0.0132,0.125) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)
Lutjanus johni	r ~ lognormal(-1.4741,4.4814))	K ~ uniform(1180,59000)	pi ~ uniform(0.019,0.116) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)
Lutjanus malabaricus	r ~ lognormal(-1.2447,4.4814)	K ~ uniform(704,35200)	pi ~ uniform(0.012,0.14) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)
Otolithes ruber	r ~ lognormal(-1.9888,4.4814)	K ~ uniform(4187,209350)	pi ~ uniform(0.01,0.135) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)
Pampus argenteus	r ~ lognormal(-0.5547,4.4814)	K ~ uniform(569,28450)	pi ~ uniform(0.014,0.132) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)
Parastromateus niger	r ~ lognormal(-1.8574,4.4814)	K ~ uniform(6456,322800)	pi~uniform(0.01,0.121) pm=log(pi) P[1]~lognormal(pm, $1/\sigma^2$)
Platycephalus indicus	r ~ lognormal(-2.0425,4.4814)	K ~ uniform(1076,53800)	pi ~ uniform(0.0126,0.113) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)
Pomadasys kaakan	r ~ lognormal(0.0615,4.4814)	K ~ uniform(2992,149600)	pi ~ uniform(0.01,0.114) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)
Protonibea diacanthus	r ~ lognormal(-1.0531,4.4814)	K ~ uniform(4429,221450)	pi ~ uniform(0.0171,0.1587) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)
Saurida tumbil	r ~ lognormal(-0.9886,4.4814)	K ~ uniform(2170,108500)	pi ~ uniform(0.0154,0.1286) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)
Scomberoides commersonnianus	r ~ lognormal(-1.5099,4.4814)	K ~ uniform(11001,55005)	pi ~ uniform(0.0194,0.105) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)
Rhabdosargus sarba	r ~ lognormal(-1.0634,4.4814)	K ~ uniform(1746,87300)	pi ~ uniform(0.0164,0.1613) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)
Trachinotus mookalee	r ~ lognormal(-1.7514,4.4814)	K ~ uniform(712,35600)	pi ~ uniform(0.0163,0.12) pm = log(pi) P[1] ~ lognormal(pm, $1/\sigma^2$)

The stock biomass at which the maximum sustainable yield (MSY) was attained (B_{MSY}) is given as Equation 6:

$$B_{MSY} = K(z + 1)^{(-1/z)} \tag{6}$$

whilst, F_{MSY} is the fishing mortality corresponding to MSY and is described as Equation 7:

$$F_{MSY} = K(z + 1)^{(-1/z)} \tag{7}$$

The related value of MSY is calculated as Equation 8:

$$MSY = B_{MSY}F_{MSY} = K(z + 1)^{(-1/z)}.r(z + 1)^{(-1/z)} = Kr(z + 1)^{(-2/z)} \tag{8}$$

Finally, the relative fishing mortality rate F_S and relative biomass B_S are assessed by $F_S = F_t / F_{MSY}$ and $B_S = B_t / B_{MSY}$, respectively.

Model fitting

The Bayesian state-space combines the joint prior distributions of all parameters and unobservable conditions with the likelihood functions of the observations (Brodziak and Ishimura 2011; Meyer and Millar 1999; Punt and Hilborn 1997). Due to the conditional independence between the model parameters and unobserved conditions, the joint posterior distribution of the unobservable data, (p(K, r, q, z, σ^2, τ^2, P_1,..., P_N | I_1, ... , I_N)), is proportional to the joint posterior distribution of all un-observables and observables (Meyer and Millar 1999; Montenegro and Branco 2016; Rankin and Lemos 2015) formulated as Equation 9:

$$p(\mathrm{K}, \mathrm{r}, \mathrm{q}, \mathrm{z}, \sigma^2, \tau^2, P_1, \ldots, P_n, I_1, \ldots, I_n) = [K] \times [r] \times [q] \times [z] \times [\sigma^2] \times [\tau^2] \times [P_1|\sigma^2]$$
$$\times \prod_{t=2}^{N} p(P_t|P_{t-1}, K, r, z, \sigma^2) \times \prod_{t=1}^{N} p(I_t|P_t, K, q, \tau^2) \tag{9}$$

with square brackets indicating densities and N referring to the number of samples. Supplementary information on the above-mentioned general factorisation of Bayesian model (Eq. 9) is available in Wikle et al. 1998 and Clark and Gelfand 2006.

The Markov chain Monte Carlo (MCMC) algorithm using Gibbs sampling was used to explore the joint posterior distributions of the parameters and un-observable states. OpenBugs software (v3.2.3) (Thomas et al. 2006) was used for simulations and was run within R using the R2OpenBugs package (Sturtz et al. 2010). Three chains of 100,000 iterations used to estimate parameters for the model of each fish species. The first 50,000 iterations of each chain were discarded to remove any dependence on initial parameter values; as well, random initial values were generated for each chain. The resulting 50,000 samples were thinned at a rate of 1:5 to remove autocorrelation. This results in a sample size of 10,000 per chain to assess the summary statistics of parameter posterior distributions. Model convergence was assessed with the convergence diagnostics of Geweke (Geweke 1991), Gelman–Rubin's potential scale reduction measure (Gilks et al. 1996) and Heidelberger and Welch stationarity (Heidelberger and Welch 1983), calculated using the R-package CODA (Plummer et al. 2006).

Results and discussion

In line with the aims of the current research, the results of Bayesian state-space GSPM from MCMC simulations are briefly presented in Tables 3–4 and Figures 2–3 for the fourteen specified high-commercial demersal fish species in the study area. In addition, the related results are described and discussed as follows:

Convergence to posterior distribution

Table 2 presents the outcomes of three tests for model diagnosis about convergence and stationarity (Plummer et al. 2006).

In the first place, the Geweke diagnostic test was separately applied to verify convergence of the mean of each parameter obtained from the sampled values related to each single chain. In the following, the derived Z-score indicates convergence if its values be less than 2 at absolute value. Thus, as shown in Table 2, for three MCMC chains of all fourteen specified high-commercial demersal fish species, the absolute value of Z-scores is less than 2 which demonstrates that there are no considerable differences in the means of the first and last collections of iterations of the chains. Secondly, the potential scale reduction factor of the Gelman-Rubin diagnostic ($\hat{R}$) is used to investigate the convergence of the chain applying two or more samples produced in parallel. The $\hat{R}$values, approximately close to one, which reveal convergence shows that all MCMC samples of the model parameters reached convergence to posterior distributions. Therefore, according to the results, the $\hat{R}$values are identically one for all the above-mentioned fish species MCMC chains, which are consistent with the convergence in distribution of the MCMC samples to the posterior distributions. The third diagnostic statistic, the Heidelberger-Welch stationarity test, was used to explore the sample convergence of single chains from univariate observations, expressed by p-values. Hence, considering the results, the MCMC chains of all the fish species MCMC simulations passed the Heidelberger and Welch stationarity test, which could not reject the hypothesis that the MCMC chains are stationary at the 95% confidence level for any of the parameters. Generally, the above-described diagnostic convergence tests and visual consideration of trace plots in Appendix 2, confirm that the MCMC chains of all fourteen specified high-commercial demersal fish species produce representative specimens from the joint posterior distribution over the model parameters.

Table 2. Convergence and stationarity diagnostics of MCMC algorithm for bayesian state-space gspm fourteen specified high-commercial demersal fish species.

Species	Geweke's Z-score									Gelman-Rubin			Heidelberger-Welch's p-value								
	Chain 1			Chain 2			Chain 3			Potential scale reduction factor ($\hat{R}$)			Chain 1			Chain 2			Chain 3		
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Chain 1	Chain 2	Chain 3	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
Elutheronema tetradactylum	-1.73	1.48	0.228	-1.86	1.62	-0.065	-1.72	1.452	0.135	1	1	1	0.006	0.9	0.383	0.05	0.9	0.546	0.027	0.97	0.4
Lethrinus microdon	-1.7	1.36	0.245	-1.64	1.08	0.09	-1.66	1.61	0.174	1	1	1	0.014	0.9	0.496	0.054	0.96	0.568	0.053	0.98	0.4
Lutjanus johni	-1.36	1.13	0.227	-1.14	1.48	-0.129	-1.7	1.36	0.22	1	1	1	0.004	0.95	0.447	0.058	0.91	0.513	0.052	0.99	0.68
Lutjanus malabaricus	-1.33	1.261	0.06	-1.6	1.612	-0.05	-1.02	1.51	0.407	1	1	1	0.03	0.99	0.67	0.05	0.99	0.486	7E-6	0.99	0.71
Otolithes ruber	-1.79	1.365	0.068	-1.55	1.52	0.252	-1.77	1.4	0.264	1	1	1	0.007	0.99	0.619	0.007	0.99	0.568	0.07	0.98	0.477
Pampus argenteus	-1.83	1.9	0.195	-1.01	1.03	0.188	-1.47	1.43	0.345	1	1	1	0.01	0.98	0.649	0.05	0.99	0.512	0.056	0.99	0.677
Parastromateus niger	-1.06	1.98	0.181	-1.47	1.37	0.11	-1.45	1.84	0.02	1	1	1	0.05	0.98	0.391	0.05	0.98	0.44	0.01	0.99	0.412
Platycephalus indicus	-1.25	1.56	0.11	-1.15	1.9	0.11	-1.35	1.61	0.232	1	1	1	0.05	0.99	0.39	0.06	0.99	0.44	0.006	0.99	0.61
Pomadasys kaakan	-1.11	1.91	0.018	-1.63	1.3	0.251	-1.88	1.06	0.268	1	1	1	0.01	0.99	0.7	0.07	0.95	0.49	0.002	0.99	0.62
Protonibea diacanthus	-1.27	1.03	0.226	-1.1	1.35	0.33	-1.14	1.8	-0.02	1	1	1	0.007	0.98	0.623	0.05	0.99	0.476	0.008	0.99	0.592
Saurida tumbil	-1.18	1.11	0.035	-1.18	1.78	0.007	-1.08	1.24	0.176	1	1	1	0.05	0.99	0.49	0.07	0.97	0.34	0.06	0.98	0.57
Scomberoides commersonnianus	-1.19	1.14	0.19	-1.13	1.69	0.126	-1.04	1.53	0.204	1	1	1	0.05	0.9	0.5	0.007	0.99	0.297	0.05	0.95	0.48
Rhabdosargus sarba	-1.25	1.51	0.13	-1.23	1.21	0.12	-1.04	1.07	0.048	1	1	1	0.05	0.9	0.5	0.05	0.9	0.5	0.02	0.98	0.61
Trachinotus mookalee	-1.89	1.62	0.024	-1.2	1.72	0.242	-1.55	1.25	0.093	1	1	1	0.05	0.98	0.36	0.05	0.99	0.417	0.017	0.96	0.5

Estimates of model parameters

Summary of the posterior descriptive statistics is presented in Table 3, including the posterior means and marginal posteriors with 95% credibility intervals (Crl) (the 2.5% and 97.5% percentiles as lower and upper limits) for Bayesian state-space GSPM parameters of the fourteen specified high-commercial demersal fish species.

Since the intrinsic growth rate *r* shows the relationship between size and age, it is an important factor in life history theory (Arendt 1997). The marginal posterior means of the intrinsic growth rate (r) for *Elutheronema tetradactylum* within 95% credibility intervals (0.051, 0.332) indicated that the given available data information (prior distribution) and the true value of (r) falls within (Crl) with 95% probability. Similarly, for all other thirteen fish species, the marginal posterior means of (r) were within 95% credibility intervals of the posterior predictive distributions and it can be concluded that, for the given available data information (prior distribution), the true value of (r) falls within (Crl) 95% probability for them. The posterior means of intrinsic growth rate for *Platycephalus indicus* and *Scomberoides commersonnianus* were similar to results attained by Cheung and Sumaila (2015), but for all the other 11 remaining fish species, except for *Protonibea diacanthus*, the posterior means of intrinsic growth were lower and, for *Protonibea diacanthus*, it was more than the results of the recently above-mentioned study. The posterior means of all the fish species more than medians indicates that their posterior distributions right skewed. Since the mean and median of posterior distribution of (r) for all fish species was within 95% (Crl), therefore for the given available data information (prior distribution), the true value of (r) falls within (Crl) with 95% probability.

According to the results in Table 3, the marginal posterior means of shape parameter, (z), for *Elutheronema tetradactylum* was within the 95% credibility intervals (0.112, 2.736), indicating that, for the given available data information (prior distribution), the true value of (z) falls within (Crl) with 95% probability. Similarly, for all other thirteen fish species, the marginal posterior means of (z) were within the 95% credibility intervals of the posterior predictive distributions and it can be concluded that, for the given available data information (prior distribution), the true value of (z) falls within (Crl) with the 95% probability for them. In addition, based on the results, for all Bayesian state-space GSPM, the marginal posterior means for (*z*), with 95% credible interval, were dissimilar and the posterior means greater than medians indicated that the related posterior distributions were right skewed. The posterior means of shape parameter *z* for *Platycephalus indicus* and *Scomberoides commersonnianus* were more than unity and indicates that the biomass production was increased into peak when the biomass was more than K/2. However, for all the other remaining 12 fish species, the posterior means and medians of shape parameter *z* were less than unity, indicating that the biomass production peaked when the biomass was less than K/2. As mentioned above and according to the results of Table 3, although the value of the shape parameter *z* is different from unity for all 14 models, due to the proximity of the value of *z* with unity, it may be assumed that the classic Schaefer (logistic) surplus

Table 3. A summary of the posterior descriptive statistics for bayesian state-space GSPM parameters of fourteen specified high-commercial demersal fish species.

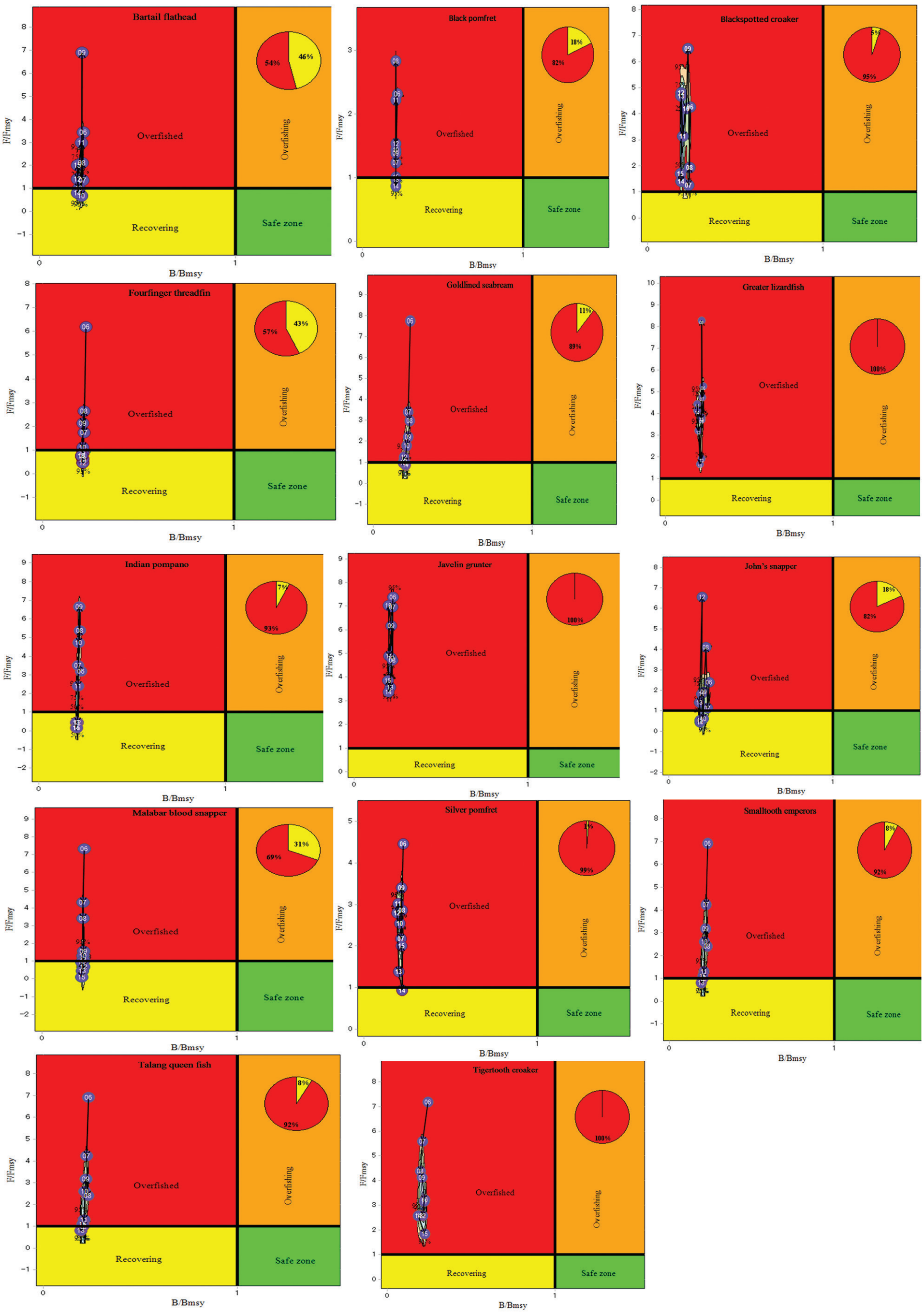
Parameter		Species						
		Elutheronema tetradactylum	***Lethrinus microdon***	***Lutjanus johni***	***Lutjanus malabaricus***	***Otolithes ruber***	***Pampus argenteus***	***Parastromateus niger***
r	Mean	0.329	0.727	0.248	0.298	0.152	0.612	0.34
	S.D.	0.141	0.286	0.113	0.134	0.074	0.279	0.161
	MC error	0.001	0.004	0.001	0.001	9.8E-4	0.002	0.001
	Perc. 2.5%	0.126	0.295	0.09	0.111	0.054	0.223	0.124
	Median	0.304	0.688	0.223	0.273	0.137	0.558	0.306
	Perc. 97.5%	0.668	1.393	0.529	0.627	0.336	1.295	0.748
K	Mean	1058	1530	1995	1110	5175	1409	12080
	S.D.	365.6	370	623.6	353	908.7	553.5	5477
	MC error	2.726	3.717	6.953	2.64	18.11	5.416	51.99
	Perc. 2.5%	621.5	1104	1214	718.1	4215	634.5	6602
	Median	975.7	1438	1865	1017	4918	1318	10450
	Perc. 97.5%	1975	2463	3526	2018	7565	2736	26630
q	Mean	0.001	0.001	0.001	0.001	0.001	0.001	5.5E-4
	S.D.	5E-4	3E-4	4.4E-4	4.2E-4	1.5E-4	7.2E-4	1.9E-4
	MC error	4E-6	3E-6	4.5E-6	3E-6	3E-6	6.5E-6	1.7E-6
	Perc. 2.5%	8E-4	8.8E-4	8.4E-4	8.3E-4	6.9E-4	8.5E-4	2E-4
	Median	0.001	0.001	0.001	0.001	0.001	0.001	5.5E-4
	Perc. 97.5%	0.002	0.002	0.002	0.002	0.001	0.003	9.2E-4
z	Mean	0.953	0.89	0.995	0.96	0.993	0.987	0.983
	S.D.	0.708	0.661	0.709	0.688	0.695	0.712	0.698
	MC error	0.006	0.008	0.008	0.005	0.012	0.006	0.005
	Perc. 2.5%	0.112	0.108	0.119	0.117	0.122	0.118	0.121
	Median	0.779	0.723	0.829	0.795	0.84	0.821	0.82
	Perc. 97.5%	2.736	2.604	2.808	2.707	2.728	2.776	2.766
σ^2	Mean	0.007	0.007	0.008	0.007	0.007	0.007	2.5E-4
	S.D.	0.002	0.002	0.002	0.002	0.002	0.002	1.4E-4
	MC error	1.2E-5	1.5E-5	1.6E-5	1E-5	1.3E-5	1.4E-5	8.7E-7
	Perc. 2.5%	0.004	0.004	0.004	0.004	0.004	0.004	9.8E-5
	Median	0.006	0.007	0.008	0.006	0.007	0.007	2E-5
	Perc. 97.5%	0.012	0.014	0.015	0.012	0.012	0.139	6.3E-4
τ^2	Mean	0.358	0.071	0.021	0.459	0.012	0.079	0.121
	S.D.	0.105	0.023	0.007	0.134	0.004	0.025	0.045
	MC error	6E-4	1.3E-4	4.8E-5	8E-4	2.5E-5	1.3E-4	3.2E-4
	Perc. 2.5%	0.206	0.037	0.009	0.266	0.006	0.042	0.06
	Median	0.341	0.068	0.02	0.437	0.012	0.075	0.112
	Perc. 97.5%	0.613	0.127	0.04	0.785	0.023	0.139	0.236

production model (SSPM) is a better option than the generalised surplus production model (GSPM). Therefore, the (SSPM) was estimated for all aforesaid fourteen studied fish species and compared with (GSPM) based on predictive performance using the Deviance Information Criterion (DIC), given by Spiegelhalter et al. 2002. In addition, according to Ando (2010), DIC is used to compare the performance of different Bayesian models. It is particularly useful where the posterior distributions of the mod-

Table 3. Continued.

Parameter		Species						
		Platycephalus indicus	***Pomadasys kaakan***	***Protonibea diacanthus***	***Saurida tumbil***	***Scomberoides commersonnianus***	***Rhabdosargus sarba***	***Trachinotus mookalee***
r	Mean	0.145	1.173	0.474	0.411	0.247	0.378	0.175
	S.D.	0.073	0.567	0.328	0.201	0.124	0.175	0.079
	MC error	8.3E-4	0.004	0.009	0.002	0.001	0.002	7.6E-4
	Perc. 2.5%	0.051	0.42	0.142	0.146	0.087	0.136	0.066
	Median	0.13	1.057	0.377	0.369	0.221	0.343	0.16
	Perc. 97.5%	0.332	2.598	1.314	0.92	0.561	0.806	0.367
K	Mean	1609	4015	6641	2580	11630	2146	1121
	S.D.	445.7	902.6	1876	390.6	616.1	365.3	336
	MC error	4.183	6.027	28.51	4.339	6.865	4.086	2.851
	Perc. 2.5%	1095	3022	4504	2182	11020	1758	727.4
	Median	1498	3771	6149	2466	11450	2042	1041
	Perc. 97.5%	2734	6334	11510	3607	13270	3109	1971
q	Mean	0.001	0.001	0.001	9.5E-4	4.3E-4	0.001	0.001
	S.D.	3.4E-4	2.5E-4	3.2E-4	1.3E-4	3.2E-5	1.6E-4	4E-4
	MC error	3E-6	1.6E-6	4.9E-6	1.5E-6	5E-7	1.8E-6	3.2E-6
	Perc. 2.5%	8E-4	7.7E-4	6.8E-4	6.6E-4	3.6E-4	6.9E-4	8.4E-4
	Median	0.001	0.001	0.001	9.5E-4	4.3E-4	0.001	0.001
	Perc. 97.5%	0.002	0.001	0.001	0.001	4.9E-4	0.001	0.002
z	Mean	1.001	0.996	1.047	1.006	0.982	0.993	0.965
	S.D.	0.704	0.699	0.72	0.73	0.691	0.701	0.711
	MC error	0.005	0.005	0.01	0.011	0.012	0.007	0.005
	Perc. 2.5%	0.12	0.118	0.131	0.118	0.12	0.117	0.109
	Median	0.842	0.838	0.89	0.836	0.824	0.832	0.792
	Perc. 97.5%	2.774	2.752	2.869	2.824	2.726	2.765	2.803
σ^2	Mean	0.007	0.007	0.008	0.008	0.008	0.008	0.007
	S.D.	0.002	0.002	0.003	0.002	0.003	0.003	0.002
	MC error	1.6E-5	1.4E-5	2.3E-5	1.5E-5	1.8E-5	1.8E-5	1.2E-5
	Perc. 2.5%	0.004	0.004	0.004	0.004	0.004	0.004	0.004
	Median	0.007	0.007	0.008	0.007	0.008	0.007	0.007
	Perc. 97.5%	0.014	0.013	0.017	0.014	0.016	0.015	0.012
τ^2	Mean	0.068	0.082	0.027	0.056	0.028	0.046	0.145
	S.D.	0.022	0.026	0.01	0.019	0.011	0.016	0.044
	MC error	1.3E-4	1.4E-4	1E-4	1E-4	7.6E-5	9.9E-5	2.4E-4
	Perc. 2.5%	0.035	0.044	0.01	0.028	0.012	0.022	0.08
	Median	0.064	0.078	0.026	0.053	0.026	0.044	0.138
	Perc. 97.5%	0.122	0.146	0.053	0.102	0.055	0.085	0.252

els have been obtained by MCMC algorithm estimation. Therefore, while comparing different possible models for their similar records, lesser values of DIC recommend better predictive capability. Thus, according to the results of Table 4, the value of DIC for all fish species, based on GSPM, is less than that of SSPM. Therefore, GSPM is more suitable for analysing the present study.


Bartail flathead

Black pomfret

Blackspotted croaker

Fourfinger threadfin

Goldlined seabream

Greater lizardfish

Indian pompano

Javelin grunter

John's snapper

Malabar blood snapper

Silver pomfret

Smalltooth emperors

Talang queen fish

Tigertooth croaker

Figure 2. Phase diagram depiction of F/F$_{MSY}$ and B/B$_{MSY}$ for fourteen specified highcommercial demersal fish species, each panel is designate by the common name of the fish at the top. The numbers on purple circles represent the last two digits of the year related to abovementioned ratios.

The results of Table 3 identify that the marginal posterior means of carrying capacity, (K), for *Elutheronema tetradactylum* was within the 95% credibility intervals (621.5, 1975) and indicates that, for the given available data information (prior distribution), the true value of (K) falls within (Crl) with 95% probability. Similarly, for all other thirteen fish species, the marginal posterior means of (K) were within the 95% credibility intervals of the posterior predictive distributions and it can be concluded that, for the given available data information (prior distribution), the true value of (K) falls within (Crl) with 95% probability for them. The posterior means of carrying capacity *K* with 95% credibility intervals more than the medians as reveals that the posterior distributions right skewed.

The marginal posterior means of the catchability coefficient (q) for *Elutheronema tetradactylum* was within the 95% credibility intervals (0.0008, 0.002) and indicates that, for the given available data information (prior distribution), the true value of (q) falls within (Crl) with 95% probability. Similarly, for all other thirteen fish species, the marginal posterior means of (q) were within the 95% credibility intervals of the posterior predictive distributions and it can be concluded that for the given available data information (prior distribution), the true value of (q) falls within (Crl) with 95% probability for them. Furthermore, the posterior means and medians of the catchability coefficient (*q*) with 95% confidence interval for all the studied fish species were equal which shows that their posterior distributions were symmetric.

The marginal posterior means of the process noise variances, (Σ^2) for *Elutheronema tetradactylum* was within the 95% credibility intervals (0.004, 0.012) and indicates that, for the given available data information (prior distribution), the true value of (Σ^2) falls within (Crl) with 95% probability. Similarly, also, for all other thirteen fish species, the marginal posterior means of (Σ^2) were within the 95% credibility intervals of the posterior predictive distributions and it can be concluded that, for the given available data information (prior distribution), the true value of (Σ^2) falls within (Crl) with 95% probability for them. In addition, for the process noise variances of Bayesian state-space GSPM of *Lutjanus malabaricus, Parastromateus niger, Saurida tumbil* and *Rhabdosargus sarba* with 95% confidence interval, the posterior means were generally higher than the medians because their posterior distributions were right skewed. However, for the other 10 fish species, the posterior means and medians of the process noise variances ó^2 were equal which shows that their posterior distributions were symmetric.

The marginal posterior means of the observation noise variances, (τ^2) for *Elutheronema tetradactylum* within 95% credibility intervals (0.206, 0.613), indicates that for the given available data information (prior distribution), the true value of (τ^2) falls within (Crl) 95% probability. Similarly, for all other thirteen fish species, the marginal posterior means of (τ^2) were within 95% credibility intervals of the posterior predictive distributions and it can be concluded that, for the given available data information (prior distribution), the true value of (τ^2) falls within (Crl) with 95% probability for them. In addition, the means and medians marginal posterior of observation noise variances (τ^2) of Bayesian state-space GSPM, except for *Otolithes ruber*, were dissimilar for the other species. For the above-considered fish species, the equality of the poste-

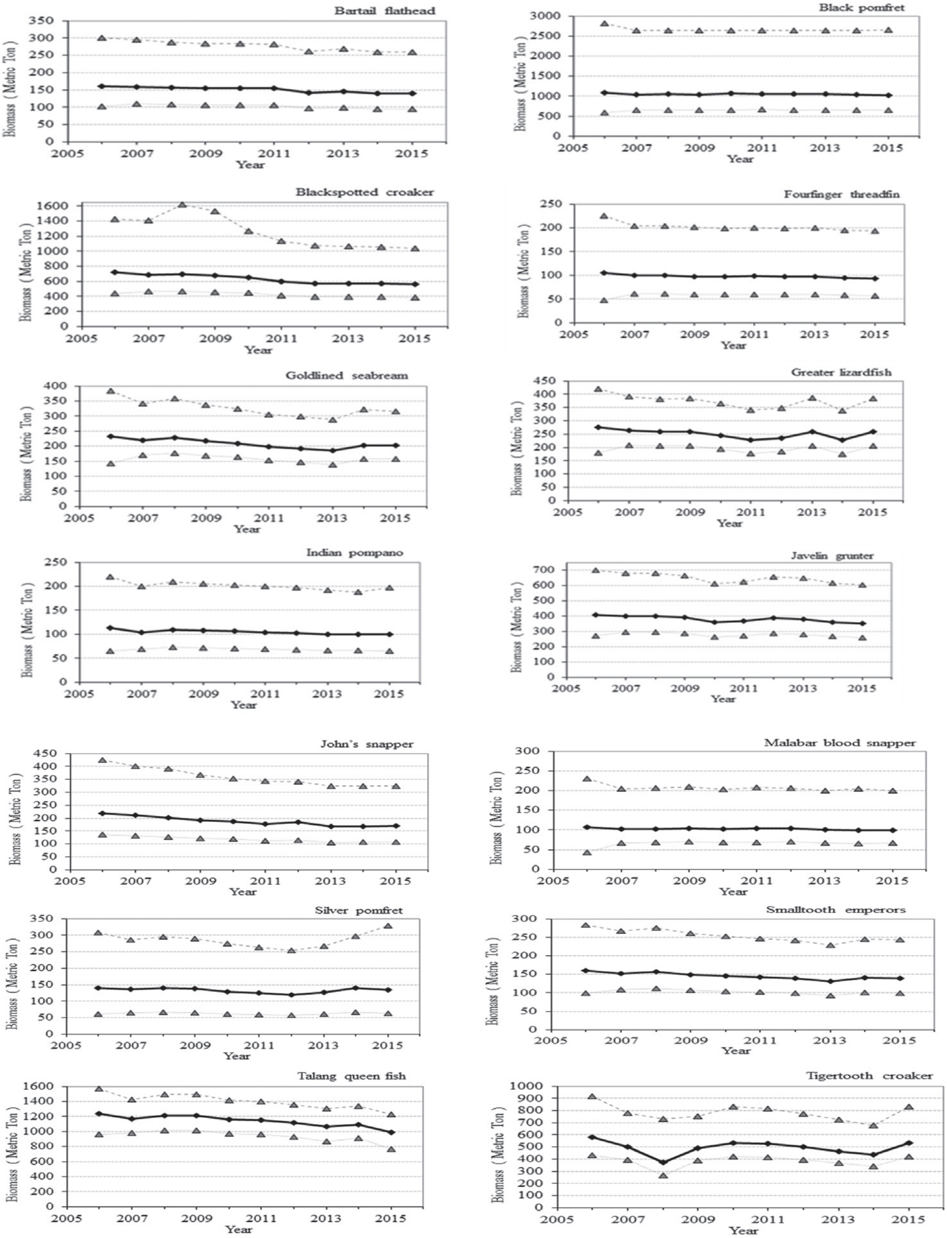


Figure 3. Simulated biomass time series (solid line with squares) of fourteen specified highcommercial demersal fish species, with 95 % confidence intervals (grey dashed and dotted lines with triangle).

rior mean and median of observation noise variances (τ^2) indicates that their posterior distributions were symmetric. However, for all the other remaining 13 fish species, due to the right skewed of their posterior distributions, the means were generally higher than the medians.

Table 4. A summary of model selection information between Generalised Surplus Production Model (GSPM) and Classic Schaefer (logistic) Surplus Production Model (SSPM) based on predictive performance using Deviance Information Criterion (DIC) for fourteen studied demersal fish species.

Species	Models	
	GSPM	SSPM
	Total DIC	Total DIC
Elutheronema tetradactylum	1.52	3.07
Lethrinus microdon	10.48	12.38
Lutjanus johni	22.33	25.59
Lutjanus malabaricus	2.352	3.87
Otolithes ruber	20.73	25.47
Pampus argenteus	7.267	9.49
Parastromateus niger	6.68	8.38
Platycephalus indicus	11.24	13.14
Pomadasys kaakan	7.14	8.96
Protonibea diacanthus	2.65	6.16
Saurida tumbil	11.82	13.92
Scomberoides commersonnianus	8.68	10.98
Rhabdosargus sarba	15.97	18.52
Trachinotus mookalee	8.02	9.68

Estimates of reference points

A summary of the results of fisheries management reference points derived from Bayesian state-space GSPM is graphically presented for all fourteen specified high-commercial demersal fish species through the stock status plots (i.e. Kobe plots or phase diagrams) in Figure 2; as well, time series of posterior median biomass with confidence intervals is shown in Figure 3.

The Kobe plot characterises, relative biomass ($B_S = B / B_{MSY}$) and relative fishing mortality rate ($F_S = F / F_{MSY}$) in a graph which provides four different quadrants, each indicating a different population status. The red region is kept for the worst case in which the stock is excessively overfished ($B / B_{MSY} < 1$) and, at the same time, the overfishing is at a high rate ($F / F_{MSY} > 1$). The green zone denotes a situation where no overfishing is happening ($F / F_{MSY} < 1$) and where the stock is not overfished ($B / B_{MSY} > 1$), so it is the best condition for the stock. The orange quadrant presents a situation where overfishing is occurring ($F / F_{MSY} > 1$), while the stock is not overfished ($B / B_{MSY} > 1$), so a decrease in fishing intensity would bring it back to the ideal green condition. The yellow subdivision shows that the stock has been overfished ($B / B_{MSY} < 1$), while the overfishing has not occurred ($F / F_{MSY} < 1$), so it will recover in due course if the fishing intensity is continued at the existing level.

According to Figure 2, the stock status of Greater lizardfish (*Saurida tumbil*), Javelin grunter (*Pomadasys kaakan*) and Tigertooth croaker (*Otolithes ruber*) are completely (100%) in the red zone. Therefore, these stocks are being excessively overfished and are threatened with extinction. The other situation of fish species, despite being overfished in recent years, is in the yellow subdivision, which indicates that these stocks are not being overfished. So, they will recover in due course if the fishing intensity continues at the existing level. Amongst them, the recovery condition of Bartail flathead (*Platycephalus indicus*), Fourfinger threadfin (*Elutheronema tetradactylum*), Malabar blood snapper (*Lutjanus malabaricus*), Black pomfret (*Parastromateus niger*) and John's snapper (*Lutjanus johni*), is much better due to their high percentage in the yellow zone. Additionally, in terms of recovery condition, the Goldlined seabream (*Rhabdosargus sarba*), Smalltooth emperors (*Lethrinus microdon*), Talang queen fish (*Scomberoides commersonnianus*) and Blackspotted croaker (*Protonibea diacanthus*) because of their less percentage in the yellow zone are in the second place. Finally, the Silver pomfret (*Pampus argenteus*) with one percentage in the yellow zone has the worst recovery situation. It can be said that it is located in the red zone and is threatened with extinction. It is noteworthy that the overfishing and overfished results of the described demersal fish species in this research were similar to those previously described (Valinassab et al. 2010; Valinassab et al. 2003; Valinassab et al. 2006; Valinassab et al. 2005). These results about the overfishing and overfished demersal fish species are also similar to those by Osio et al. 2015 who expressed that 95% of the assessed and potentially 98% of the unassessed demersal fish are overexploited. Therefore, regarding the above-described conditions, the fish species extinction may be a possibility in the future.

Simulated biomass time series of the fourteen specified high-commercial demersal fish species with 95% confidence intervals are considerable as shown in Figure 3.

According to the above-described results of the Kobe diagrams, in which all stocks are in critical condition and are threatened with extinction, the trend plots of simulated biomass confirm the previous results, due to the Biomass not having a good increasing trend. As the charts in Figure 3 show, the quantity of Biomass has not improved in recent years for all specified-fish species. If these trends unfortunately continue, the species may be extinct and the livelihoods of fishermen could be lost in the near future.

Conclusion

In summary, the Bayesian state-space GSPM under the MCMC algorithm was used to assess the stocks and provide fisheries management reference points for the fourteen high-commercial demersal fish species in the coastal domain of the study area. The authority of simulations about the models' parameters and fisheries management reference points were approved by common diagnostic convergence tests. All the assessed fish stocks encountered were overfished and being overfished. The assessment outcomes, which reveals that the stock statuses of all targeted fish species were deteriorating indicates that the available fishery management strategies of small-scale fishery in the study area were not enough and new strategies associated with sustainable management were necessary.

As mentioned in the introduction, the scientific precise stock assessments have not been undertaken in Iran, especially on the southern coastal areas (such as the current study area) because of insufficient and limited information. Accordingly, it is one of the important reasons for the inefficiency of the available fishery management and conservation strategies for sustaining the studied fish species population status in the current study area. This reason is due to lack of applicable information for fisheries management and conservation planning (such as fisheries management reference points, biomass, harvest rate and stock status) that can be obtained from scientific precise stock assessments. Thus, in the short-term, the transferring of the obtained stock assessment outcomes of the current study to fisheries managers, planners and all other activists (such as fishermen) can improve the available fisheries strategies and harvesting treatments to rebuild and improve the current bad situation of studied fish species population status. Additionally, in the long run, the recommended use of the obtained stock assessment outcomes (e.g. management and biological reference points, biomass, harvest rate, stock status) for future research in line with appropriate ecosystem-based fishery management will determine the best strategies for preventing overfishing, improving, sustaining and conserving the above-overfished stocks. Hence, the obtained stock assessment outcomes in a viability theory framework to investigate various fishing scenarios for the implementation of the sustainable fishery management in the small-scale fishery sector of the current study area were used providing the details of the recommended viability theory modelling as an appropriate ecosystem-based fishery management approach in our further works.

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Appendix I

Procedure of prior distributions functions used for parameters of all Bayesian state-space GSPM

Log-normal distribution procedure for intrinsic growth rate (r)
Standard Deviation = x
Average of Intrinsic Growth Rate (r) = y
Precision of Prior = 1/log(1 + x^2)
Average of Prior = log(y) – (0.5/ Precision of Prior)
r ~ dlnorm (Average of prior, Precision of prior)
Inverse Gamma Distribution Procedure for the Process and Observation Noise Variances
Shape Parameter = x
Scale Parameter=y
Gamma ~ dgamma (x, y)
Inverse-Gamma = 1/Gamma
Log-Normal Distribution Procedure for Initial Relative Biomass P[1]
B0=the Biomass in First Time
Kmin=minimum carrying capacity is considered equal to minimum Historical catches.
Kmax= maximum carrying capacity is considered equal to ten times the minimum Historical catches.
Pi ~ dunif(B0/Kmax, B0/Kmin)

isigma= Inverse Gamma Distribution for process noise variances
Pm[1] <- log(Pi)
P[1] ~ dlnorm(Pm[1], isigma)

Appendix 2

Trace plots for Bayesian state-space GSPM parameters (r, K, q, z, (sigma), and (tau)) for fourteen studied demersal fish species. Consider figures A1–14.

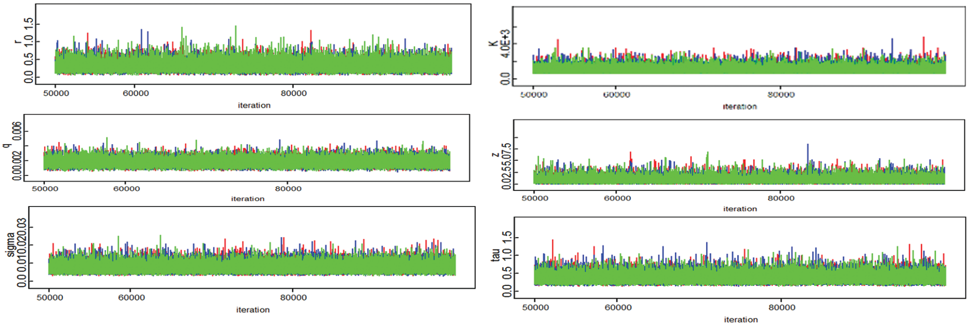

Figure A1. Trace plots for Bayesian state-space GSPM parameters of *Elutheronema tetradactylum* model.

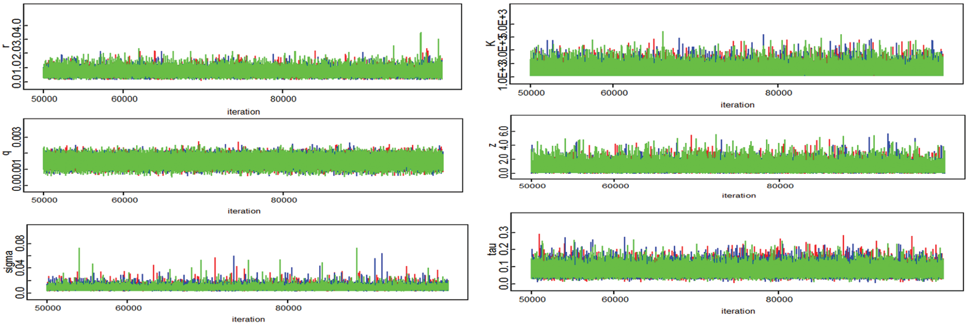

Figure A2. Trace plots for Bayesian state-space GSPM parameters of *Lethrinus microdon* model.

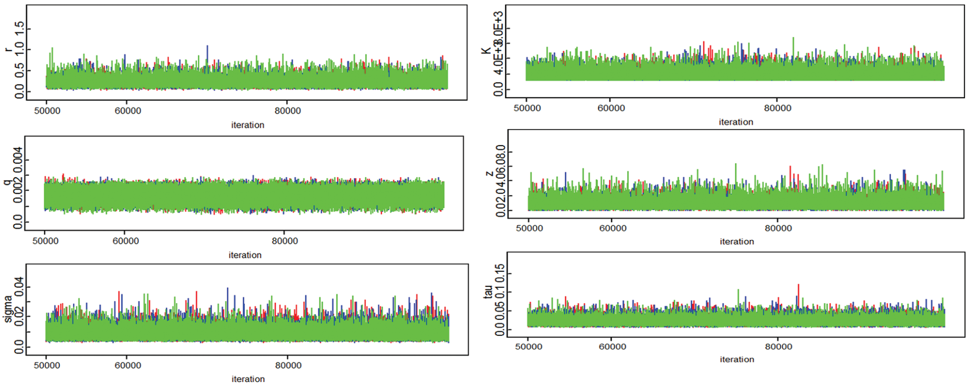

Figure A3. Trace plots for Bayesian state-space GSPM parameters of *Lutjanus johni* model.

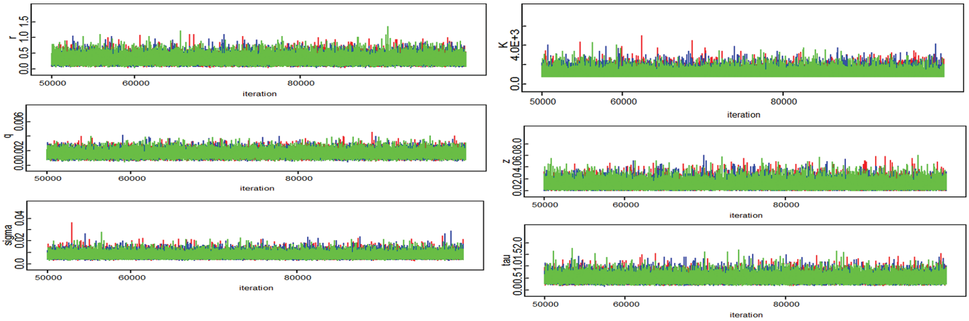

Figure A4. Trace plots for Bayesian state-space GSPM parameters of *Lutjanus malabaricus* model.

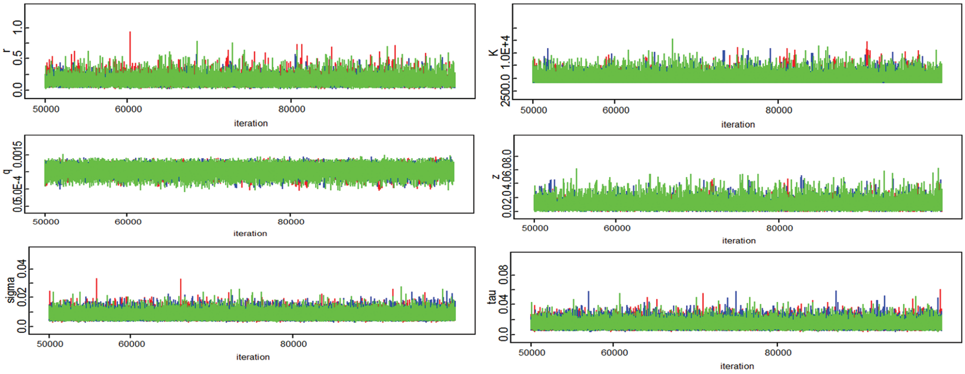

Figure A5. Trace plots for Bayesian state-space GSPM parameters of *Otolithes ruber* model.

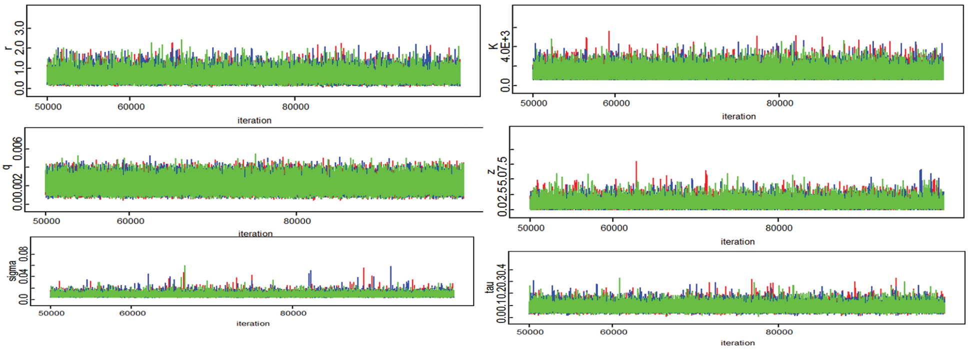

Figure A6. Trace plots for Bayesian state-space GSPM parameters of *Pampus argenteus* model.

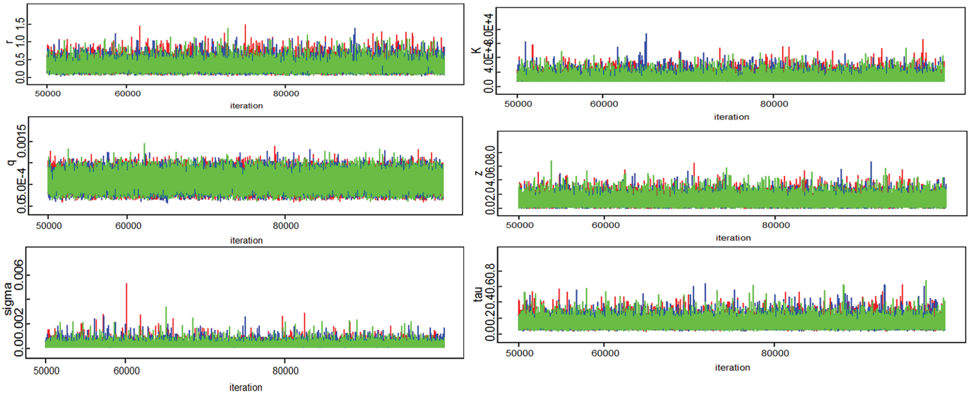

Figure A7. Trace plots for Bayesian state-space GSPM parameters of *Parastromateus niger* model.

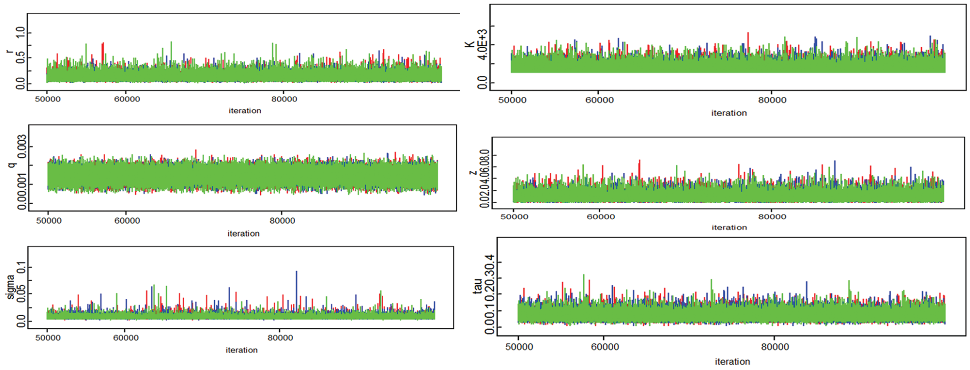

Figure A8. Trace plots for Bayesian state-space GSPM parameters of *Platycephalus indicus* model.

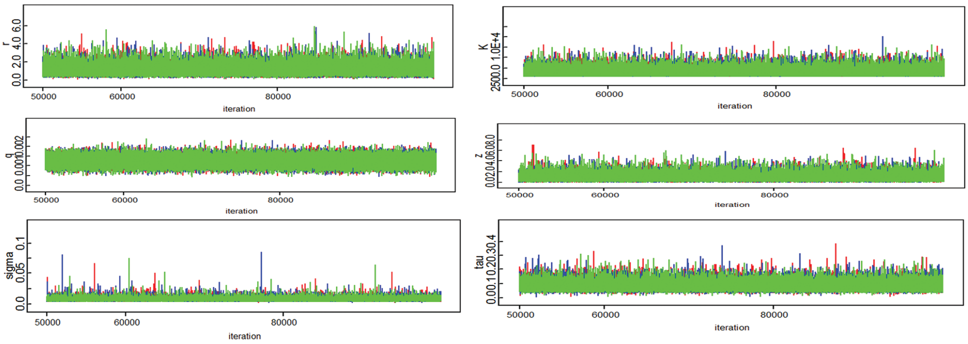

Figure A9. Trace plots for Bayesian state-space GSPM parameters of *Pomadasys kaakan* model.

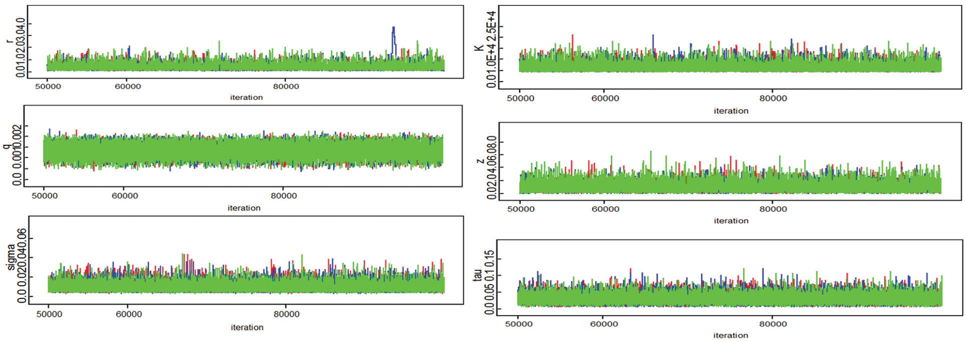

Figure A10. Trace plots for Bayesian state-space GSPM parameters of *Protonibea diacanthus* model.

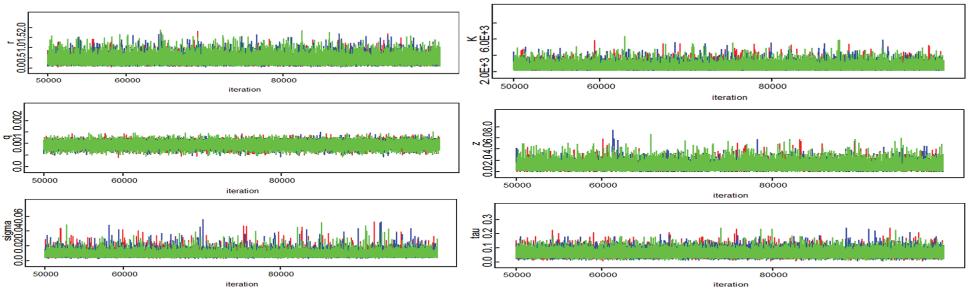

Figure A11. Trace plots for Bayesian state-space GSPM parameters of *Saurida tumbil* model.

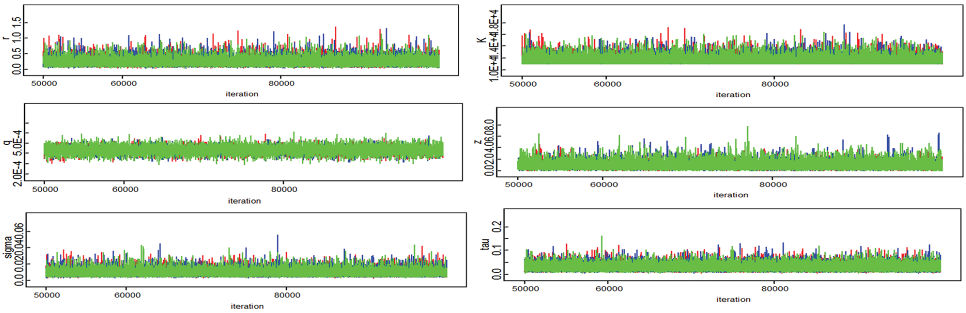

Figure A12. Trace plots for Bayesian state-space GSPM parameters of *Scomberoides* commersonnianus model.

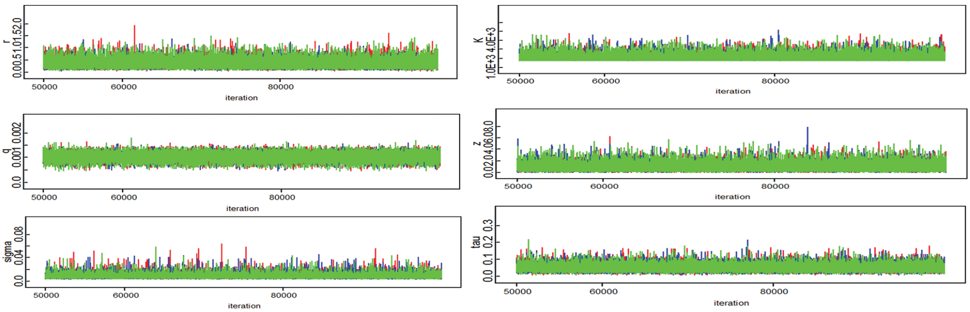

Figure A13. Trace plots for Bayesian state-space GSPM parameters of Rhabdosargus sarba model.

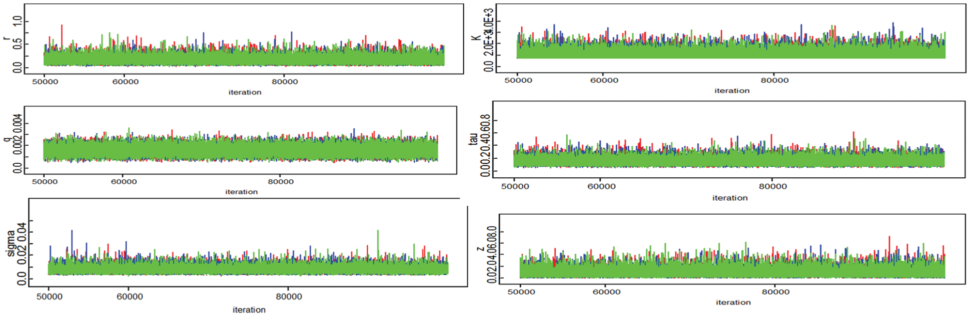

Figure A14. Trace plots for Bayesian state-space GSPM parameters of *Trachinotus* mookalee model.