

## **Review of Literature**

**Natural invertebrate aggregations in coastal and marine environments: tools used to manage populations and benefits derived from management**



Photo credit: Museums Victoria

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## Executive Summary

In Victoria there is growing interest in the appropriate management of the Australian giant spider crab *Leptomithrax gaimardii* which forms spectacular aggregations in Port Phillip Bay each year. The aggregations are thought to help protect crabs from predators while moulting. The aggregation is accessible from shore and is of great interest to recreational divers, recreational fishers, tourists, and natural history photographers and documentary makers. Careful management of the aggregation is essential due to the potential conflict of interest between some stakeholders.

To inform the development of appropriate management of the spider crab aggregations, this review considers the literature related to other marine invertebrate aggregations around the world that may be termed ‘natural wonders’. The review focuses on the instruments that have been used to manage the sustainability of these populations, and the benefits that have been derived from management. The review also focusses on the ecological, economic, social or cultural benefits associated with aggregations where they have been measured.

Species of marine invertebrates forming aggregations included in the review were: the giant Australian cuttlefish; the ornate rock lobster; the Christmas Island red crab; the northern calamari; the golden jellyfish; horseshoe crab species; and, other spider crab species. Other spider crab species do not form aggregations on the same spectacular scale as the giant spider crab but were included for comparison.

The review showed that spectacular aggregations can occur in diverse marine invertebrate groups. While most of the invertebrate aggregations reviewed are of high value for tourism and recreational diving, many are also valued as fishing species. As such, managing the sustainability of these aggregations must take into account a range of stakeholder interests and points of view.

Invertebrates in aggregations can be vulnerable to overfishing. A number of management instruments have been used to ensure the sustainability of populations. In particular, seasonal or permanent closures of the aggregation area to fishing methods to which the species are vulnerable have been used. Input and output controls to limit catches based on fishery assessments have also been applied. In one case, the declaration of a marine protected area acted as a management tool to reduce fishing pressure. Application of these management tools has generally been successful in conserving populations.

The successful management of these species has generally been underpinned by comprehensive scientific research and a detailed understanding of the species’ life history. Management has also been informed by fishery-independent monitoring, which, because of high public interest, has often been supported by a network of citizen scientists.

Management of marine invertebrate aggregations has typically involved advisory committees based on a diverse range of stakeholders. Stakeholder input and consensus can be part of an adaptive management framework where the management strategy is reviewed and, if necessary, modified on a periodic basis. Because of strong interactions between invertebrate aggregations and other ecosystem components, an ecosystem-based approach to management is considered most appropriate.

Invertebrate aggregations can have high economic value for local communities based on tourism. For example, red land crabs are the major tourist attraction on Christmas Island and golden jellyfish lakes are the major attraction for the Palau archipelago and are also a major attraction in Raja Ampat, Indonesia. In general, detailed assessments of the non-fishing economic value of invertebrate aggregations have not been undertaken.

The social and cultural benefits that can be associated with marine invertebrate aggregations are also significant. As well as economic benefits, coastal tourism and recreation and events that support them can lead to increased community awareness and understanding of the invertebrate aggregations and associated management and conservation. Social and cultural concerns of traditional users can also be incorporated into management plans based on stakeholder involvement.

## Introduction

In Victoria there is growing interest in the appropriate management of the Australian giant spider crab *Leptomithrax gaimardii* which forms spectacular aggregations in Port Phillip Bay each year (VFA 2018). Spider crabs aggregate in shallow water at various locations in south-eastern Australia over winter (Taylor and Poore 2017; VFA 2018). Aggregations are thought to be a mechanism to reduce predation impacts while moulting (Taylor and Poore 2017). Spider crabs are thought to disperse into deeper water outside the moulting aggregation season but the life history and metapopulation dynamics are poorly understood (VFA 2018).

A large aggregation of giant spider crabs has been forming annually over winter in shallow waters of the Mornington Peninsula area of Port Phillip Bay. The aggregation is accessible from local piers without the need for a boat. This aggregation is of great interest to recreational divers, recreational fishers, tourists, and natural history photographers and documentary makers (VFA 2018). The aggregation has been given international exposure through Sir David Attenborough's "Blue Planet II" documentary series. Careful management of the aggregation is essential due to the potential conflict of interest between some stakeholders.

The giant spider crab aggregation is one of a number of aggregations of marine invertebrates around the world that are considered to be "natural wonders". Information on the instruments used to manage these species (and the benefits derived), together with information on the economic (non-fisheries) and social values of these aggregations to local communities, has the potential to inform the management of giant spider crab aggregations in Port Phillip Bay.

This literature review therefore aims to provide information on the management instruments that have been put in place to conserve marine invertebrate aggregations, as well as the benefits derived from management. The review also focuses on ecological, economic, social or cultural benefits stemming from aggregations where they have been measured. The review focuses on invertebrate species which form spectacular aggregations and to which the term 'natural wonder' can be attached. The scope of the review includes marine invertebrates that aggregate to breed or moult in coastal and marine environments.

## Objectives

- To review the scientific literature on the management instruments that have been put in place to conserve marine invertebrate aggregations, including the benefits derived from management.
- To review the scientific literature on the ecological, economic, social or cultural benefits of invertebrate aggregations where they have been measured



## Review of Literature

### *Invertebrate aggregations*

#### **Giant Australian Cuttlefish**

The giant Australian cuttlefish, *Sepia apama*, is the largest species of cuttlefish in the world. It is distributed across temperate southern Australia from Moreton Bay in Queensland to Point Cloates in Western Australia, and along northern Tasmania. While abundance generally increases over inshore reefs during winter for spawning throughout the distribution, in one location in the northern Spencer Gulf a dense spawning aggregation forms that is unique amongst cuttlefish species (Hall *et al.* 2018).

Historically there was a small hand-jig fishery in the cuttlefish spawning area but this expanded rapidly from less than 5 t per annum before 1993 to over 200 t in 1996 and 1997 (Hall *et al.* 2018). In March 1998 a fishery closure was introduced to protect about half of the subtidal reef in the aggregation area. In the adjacent area that remained open, fishing started as soon as the first cuttlefish arrived in April. After 1 month of fishing a more extensive closure was introduced that encompassed the majority of the spawning habitat. This larger closure remained in place over the following four spawning seasons (from March to September) until March 2003 when it was closed to cephalopod fishing full-time (Hall *et al.* 2018). The closure to cephalopod fishing effectively banned the use of jigs but other forms of recreational fishing were allowed.

The timing and location of the cuttlefish spawning aggregation is relatively consistent from year to year making the population vulnerable to overfishing (Hall *et al.* 2018). The original closure area based on geographic features was insufficient to protect the population. An obvious and rapid within season decline was evident in the fished area after the first (partial) closure in 1998 (Hall *et al.* 2018). The larger closure area associated with a greater understanding of population biology gave significant protection, with biomass estimates increasing by 150% in the following years (Hall *et al.* 2018).

A network of marine parks was declared in South Australia in 2009 the included the Upper Spencer Gulf Marine Park (Anon. 2012). A small sanctuary zone where no fishing is allowed is located within the cephalopod fishing exclusion zone encompassing the cuttlefish spawning area.

Monitoring of cuttlefish on the spawning grounds using underwater visual transect and underwater video showed a decline in abundance from 2001, and especially from 2011, that reached a record low in 2013, indicating a 90% decline over 13 years (Steer *et al.* 2013; 2016). This decline led the species to be listed by the International Union for Conservation of Nature as 'Near Threatened'. In response to the decline the northern Spencer Gulf cuttlefish fishery was closed completely in April 2013 (Prowse *et al.* 2015). Steps were also taken to reduce the bycatch of giant cuttlefish in the spencer gulf prawn fishery (Kennelly and Broadhurst 2014; Noell *et al.* 2018). Since 2013 the spawning population has recovered to the point where the abundance estimate in 2020 was the highest on record (Anon. 2020a). As a result of the recent increase, the northern Spencer Gulf cuttlefish fishery was due to re-open in February 2021, but the spawning area closure in place since 1998 will continue.

Reasons for decline are uncertain (Steer *et al.* 2013; Prowse *et al.* 2015), but the life cycle of giant cuttlefish makes them susceptible to strong variation in recruitment success due to environmental and anthropogenic factors. Giant cuttlefish spawn once after either one or two years, depending on growth rate, and then die (semelparity) (Hall *et al.* 2007). Thus, the population trajectory has a high dependency on the survival of young (eggs and larvae) in a given year (Steer *et al.* 2013; Prowse *et al.* 2015).

Giant cuttlefish on the spawning grounds exhibit complex courtship behaviours and associated colour changes (Hall and Hanlon 2002; Schnell *et al.* 2016) that make them highly valued by tourism operators, recreational divers, and nature photographers and documentary makers. The male:female sex ratio has an average of approximately 4:1 resulting in intense competition amongst males for females (Hall and Hanlon 2002). Lone males challenge paired males for the takeover of females through dramatic agonistic displays (Hall and Hanlon 2002). Subordinate males show a never before observed behaviour in nature where they mimic the shape and colour of a female so that they can access females while dominant males are distracted when “fighting” other males (Norman *et al.* 1999; Hanlon *et al.* 2005).

There has been significant economic, social and cultural activity associated with the giant cuttlefish aggregation, particularly in Whyalla. The township runs the annual “Cuttlefest” from June to August which has a range of activities associated with the cuttlefish spawning season aimed at developing the tourism potential of the event (Anon. 2020c). This is a joint venture between the local government and tourism industry together with State government tourism and environment departments. Significant government and industry funding has been provided to improve the infrastructure and access to the spawning area for ecotourism. There is also a citizen scientist group that assists government scientists with the annual cuttlefish population census in the spawning area. A cuttlefish working group was established in 2012 to provide advice to government in relation to the ongoing protection and sustainability of the species (Anon. 2020b). To date there has not been a detailed assessment of the economic or social value of the cuttlefish in relation to tourism, recreational diving and associated sectors (M. Steer, personal communication).

## Ornate Rock Lobster

The ornate rock lobster, *Panulirus ornatus*, has a remarkable life history where, from August to September each year, adult lobsters in Torres Strait undertake a pre-spawning migration of up to 500 km to near Yule Island on the east coast of Papua New Guinea (Moore and MacFarlane 1984; Skewes *et al.* 1994). Juvenile lobsters in Torres Strait undertake their final maturation moult at between 2 and 3 years of age prior to the migration (Skewes *et al.* 1994). Lobsters can occur in very large aggregations along the migration pathway (Moore and MacFarlane 1984). Gonad development and mating occurs during the migration and spawning (release of larvae) occurs in the Yule Island area (MacFarlane and Moore 1986). The area of larval release appears to be optimal for the transport of larvae by the coral sea gyre back to the Torres Strait and the north-east Queensland coast (Dennis *et al.* 2002). Following spawning there is mass mortality of the adult lobsters on the spawning ground (Dennis *et al.* 1992).

Because migrating lobsters form large aggregations, they are vulnerable to large catches by trawlers (Ye and Dennis 2009). The spawning migration was first fished by Papua New Guinea prawn trawlers in the Gulf of Papua in the early 1970s while Australian trawlers also found the migrating lobsters further south in the Australian area of jurisdiction and began to target these lobsters in the early 1980s (Ye and Dennis 2009). In 1984, a ban on target fishing for rock lobsters by prawn trawlers was instituted in both Australia and Papua New Guinea because it was considered high vulnerability to trawling would lead to recruitment overfishing (Ye and Dennis 2009). Fishing is now restricted to methods where lobsters are taken by hand, usually by divers (Ye and Dennis 2009).

The trans-boundary sharing of the lobster stock between the two countries is governed by the Torres Strait Treaty ratified in 1985 (Pitcher *et al.* 1997). The treaty created the Torres Strait Protected Zone (TSPZ) to protect the traditional way of life and livelihood of the traditional inhabitants and specified the shares of the commercial fisheries for each party and their responsibilities for the sustainable



development of fisheries within the protected zone (Ye and Dennis 2009). Australia is entitled to take 75% of the sustainable catch from its own waters plus 25% from Papua New Guinea waters, whilst the reverse is true for Papua New Guinea.

The ornate rock lobster fishery has been managed by input controls, that differ between the indigenous and non-indigenous sectors, and include: limited entry, minimum size limit, and an annual two-month ban (October and November) on the use of hookah compressors (Pitcher *et al.* 1997; van Putten *et al.* 2013). In 2005, a Commonwealth Government decision was made to move to output controls in the fishery, including the introduction of a total allowable catch (TAC) applying at the whole fishery level, incorporating the indigenous, commercial nonindigenous and PNG catch, however this has proven difficult to implement given the complexity of the fishery (van Putten *et al.* 2013; Hutton *et al.* 2016). The management of the fishery has been underpinned by an annual diver-based survey of the abundance of lobsters (Pitcher *et al.* 1992; 1997).

The indigenous sector has both commercial and traditional subsistence components and has been heavily involved in setting the agenda for both management and research in the ornate rock lobster fishery. The fishery provides an example of how to account for socio-cultural factors in addition to biological and economic factors (triple bottom line approach) (Plagányi *et al.* 2013). This is a particularly important consideration for fisheries that are utilised by indigenous fishers or small coastal communities with high reliance on local fishery resources (Plagányi *et al.* 2018).

## Christmas Island Red Crab

On Christmas Island each year there is a spectacular migration of the terrestrial red crab, *Gecarcoidea natalis*, from their primary habitat in the rainforest to the coast for spawning (Hicks 1985; Adamczewska and Morris 2001). The breeding season lasts up to three months and the main migration begins at the onset of the wet season, usually in November or December (Hicks 1985; Adamczewska and Morris 2001). The downward migration from the plateau to the coast normally lasts 9 to 18 days (Hicks 1985). The males excavate burrows on the lowest shore terraces and mating occurs in or near the burrows (Hicks 1985; Adamczewska and Morris 2001). The males then return to the rainforest while the females remain in the burrows for two weeks until the eggs are nearly ripe (Hicks 1985). At the end of the incubation period the females make their way to shoreline rocks or sometimes the cliff faces, and release their eggs at night on the turn of the high tide between the last quarter of the moon and the new moon (Hicks 1985). The females then return in large numbers to the rainforest plateau (Hicks 1985).

Once eggs are released into the water, larvae (zoeae) hatch immediately and after passing through a number of larval stages at sea to reach the megalopae stage, they then emerge as baby crabs after approximately 1 month (Hicks 1985). Baby crabs then migrate inland, taking 9 days to reach the plateau (Hicks 1985). An aggregation of whale sharks, *Rhincodon typus*, occurs annually at Christmas Island around the time of red crab spawning and larval development, and it is thought that this aggregation is to take advantage of enhanced feeding conditions offered by the crab larvae (Meekan *et al.* 2009). This suggestion is supported by DNA analysis of faecal matter from whale sharks in the area (Meekan *et al.* 2009).

In the mid-1990's there was an estimated 43.7 million adult crabs on Christmas Island (Adamczewska and Morris 2001). This high density of crabs means that they have a significant effect on rainforest ecology and plant community structure, affecting leaf litter, seeds, fruits and seedlings (O'Dowd and Lake 1989, 1990, 1991; Green *et al.* 1997; 2008). Supercolonies of the invasive yellow crazy ant, *Anoplolepis gracilipes*, became wide-spread in the mid 1990's and were estimated to have killed 10-15 million red crabs in subsequent years (O'Dowd *et al.* 2003; Baumgartner and Ryan 2020).

The red crab breeding migration is a major attraction for naturalists, tourists, photographers and documentary film makers. The red crab migration is Christmas Island's biggest tourist attraction. A number of management actions are in place to protect the red crab population. Control of crazy ant supercolonies is mainly through heli-baiting, where helicopters are used to disperse a granular bait of the toxicant, fipronil (Baumgartner and Ryan 2020). Road closures and traffic detours are enacted across the island in the breeding season to protect the migrating crabs (Anon. 2021). Tunnels have been excavated under roads at points where a high volume of crab crossings has been identified (Anon. 2021). 'Crab bridges' have also been established to funnel crabs over busy roads (Anon. 2021).

## Northern Calamari

The loliginid squid, *Sepioteuthis lessoniana* occurs throughout tropical and subtropical waters of the Indo-West Pacific, ranging from Japan to Australia (Ching *et al.* 2019; Chiang *et al.* 2020). It has a variety of common names throughout its range, and in Australia is called the northern calamari. The northern calamari is a shallow water coastal species that requires benthic structure for the attachment of eggs when spawning (Chen *et al.* 2016).

Northern calamari grow rapidly and have a life span of around 6 to 7 months (Pecl 2001; Chen *et al.* 2015; Ching *et al.* 2019). Calamari begin to school about 30 to 60 days after hatching (Sugimoto and Ikeda 2012) and schools can comprise more than 100 individuals (Sugimoto *et al.* 2013). Calamari aggregating in spawning areas exhibit complex courtship behaviours (Lin and Chiao 2017), including signalling between individuals through colour changes (Lin *et al.* 2017).

Northern calamari support high value commercial fisheries throughout their range and are also highly targeted by artisanal and recreational fishers (Ching *et al.* 2019). In Taiwan, the species is also highly valued by recreational divers (Chen *et al.* 2016). Tourist divers can enjoy observing a school of slowly moving squid in the spawning area demonstrating a variety of interesting behaviours, such as male to male aggression, waving their large fins and tentacles, and spectacular colour changes, as well as observing their pale or semitransparent strings of eggs (Chen *et al.* 2016). Chen *et al.* (2016) stated that tourist diving trips can make a substantial contribution to the economy of northern Taiwan but did not reference any data to support this.

Commercial landings of loliginid squids off North Taiwan peaked in the mid 1990's but by the late 2000's had declined to only 25% of the level in the mid 1990's (Chen *et al.* 2016). Local recreational divers also noted that the populations of northern calamari were declining in their diving locations (Chen *et al.* 2016). Divers started placing bamboo structures at the sites that would serve as a spawning substrate and these were successful in attracting spawning calamari. Some conflict arose, however, because firstly, divers did not have government permission to deploy the structures, and, secondly, recreational fishers started targeting the structures to catch calamari (Chen *et al.* 2016). Eventually the local government implemented a permit system for individual divers to place the bamboo structure in a specified area for a six month period each year (Chen *et al.* 2016). No action has been put in place, however, to resolve the conflict between divers and recreational fishers (Chen *et al.* 2016). Chen *et al.* (2016) recommended that general (rather than) individual permission be given for the placement of structures in specified places during the spawning season. It was also recommended that these locations be closed to recreational fishing and that scientific monitoring should be undertaken. Collaborative management was recommended that would include the diving tourism industry, government, university scientists and the enforcement agency (Chen *et al.* 2016).

In Japan there is a citizen science and tourism venture where tourists help deploy habitat (tree branches) for northern calamari spawning, and then are able to observe the hatching of some eggs that were laid on the habitat in the local aquarium (Anon. 2019a).

## Golden Jellyfish

Golden jellyfish, *Mastigias* spp., occur in dense populations in some marine lakes (bodies of seawater surrounded entirely by land), and in many places have become major tourist attractions (Maas *et al.* 2020). Of the approximately 200 marine lakes known worldwide, 22 are “jellyfish lakes” and are located in Indonesia, Palau and Vietnam (Maas *et al.* 2020). Although the jellyfish do have a sting, it is seldom noticeable, and freediving with the jellyfish is extremely popular. It is estimated that in 2015 the Ongeim'l Tketau Jellyfish Lake attracted at least two-thirds of the 160,000 annual visitors to the Palau archipelago (Anon. 2019b).

The jellyfish population in Ongeim'l Tketau Lake crashed in 1998 and 2016 before recovering in the following years (Dawson *et al.* 2001; Anon. 2016, 2019b). These crashes are thought to have been caused by strong El Niño events that led to increased water temperatures in the lakes (Dawson *et al.* 2001; Anon. 2016, 2019b). Sunscreen pollution has also been implicated in the recent decline but not proven (Anon. 2019b; Maas *et al.* 2020). A major tourism drop occurred after the crash in 2016 as tourism operators voluntarily stopped taking tourists to the lake (Anon. 2019b). Four other marine lakes that contain golden jellyfish in Palau are not open to the public (Anon. 2019b).

The golden jelly fish lakes in Raja Ampat Indonesia are not included in marine protected area planning as only areas below the high tide mark are included (Maas *et al.* 2020). The seven individual jellyfish lakes in Raja Ampat have endemic genotypes and phenotypes of jellyfish, including potentially undescribed subspecies (Maas *et al.* 2020). At the same time, tourism has increased 30-fold since 2007, and the jellyfish lakes are one of the main attractions. Mass *et al.* (2020) recommend including the marine lakes in the Raja Ampat Marine Protected Area (MPA) zoning system, and, the establishment of a collaboration between indigenous communities, local tenure holders, the Raja Ampat MPA Management Authority and Raja Ampat Tourism Department, conservation NGOs, and researchers to develop a specific Raja Ampat Jellyfish Lake Management Plan.

## Horseshoe Crabs

Horseshoe crabs are marine arthropods that are more closely related to arachnids (e.g. spiders and scorpions) than they are to decapod crustaceans (e.g. crabs) (Smith *et al.* 2017; John *et al.* 2018). Horseshoe crabs are “living fossils” that have remained largely unchanged for 200 million years, and have an evolutionary lineage going back over 500 million years (Smith *et al.* 2017; John *et al.* 2018). World-wide there are four species of horseshoe crabs, three species, *Tachypleus tridentatus*, *Tapinauchenius gigas* and *Carcinoscorpius rotundicauda*, are found in south east Asian waters from India to Japan, while *Limulus polyphemus* is found along the Atlantic coast of the USA and Mexico (John *et al.* 2018).

Horseshoe crabs aggregate at the edge of intertidal zones on sandy beaches for spawning (Ehlinger *et al.* 2003). *Limulus Polyphemus* deposit their eggs between the tidal flat and the high-water line, generally around the time of high tide and in some cases coinciding with new and full moons (Landi *et al.* 2015; Smith and Robinson 2015; Smith *et al.* 2017). Females excavate a shallow nest in the sand and deposit clusters of up to approximately 6,000 eggs that are subsequently fertilised by an attached male and one or more satellite males (Ehlinger *et al.* 2003; Smith *et al.* 2017). The eggs and newly-hatched

larvae of horseshoe crabs provide an important food source for a variety of animals including endangered migratory shorebirds (McGowan *et al.* 2011; 2015; Smith *et al.* 2017)

The spawning aggregations of horseshoe crabs on beaches are a spectacular sight, but this also makes them vulnerable to exploitation. Historically, horseshoe crabs (*Limulus Polyphemus*) in the Delaware Bay area were collected to be used for agricultural fertiliser but this practice declined to a negligible level by the 1960's (Smith *et al.* 2017; Krisfalusi-Gannon *et al.* 2018). Thereafter, the use of horseshoe crabs as bait in the American eel and whelk pot fisheries led to a rapid increase in horseshoe crab take in the 1990s (Smith *et al.* 2017; Krisfalusi-Gannon *et al.* 2018). Evidence suggests that overharvest can result in depleted populations and localised removal (Smith *et al.* 2017). Since 1998, management instruments such as set harvest quotas and season closures, as well as establishment of a national marine reserve offshore from the bay, have acted to substantially reduce the level of catch (Smith *et al.* 2017).

Overharvest of horseshoe crabs in Delaware Bay was a major concern in relation to feeding by shorebirds, particularly the endangered red knot (Tan and Jardine 2019). These birds stop over and feed on horseshoe crab eggs on their way from South America to the Arctic breeding grounds (Tan and Jardine 2019). The migratory shorebirds are highly valued by bird watchers, and the congregation of birds and hermit crabs is a valuable tourist attraction, estimated to be worth between \$200 – 300,000 USD in 2008 dollars per six week season annually (Myers *et al.* 2010; Edwards *et al.* 2011). The interaction with migratory shorebirds is a major consideration in the management of horseshoe crab harvest (McGowan *et al.* 2015; Tan and Jardine 2019). An adaptive management approach has been taken in relation to the horseshoe crab harvest that considers the shorebirds as well as the crabs, and involves a diverse group of stakeholders in an attempt to reach consensus when choosing between different horseshoe crab harvest strategies based on modelling studies (McGowan *et al.* 2011; 2015). The management of the horseshoe crab harvest in Delaware Bay has been underpinned by an ongoing monitoring program based on an extensive citizen science network (Smith and Robinson 2015).

Another form of exploitation is the use of horseshoe crab blood in the pharmaceutical and biomedical industries (Krisfalusi-Gannon *et al.* 2018). The light blue blood of the horseshoe crab contains amebocytes that produce an instantaneous, visible reaction to bacterial endotoxin (Smith *et al.* 2017; Krisfalusi-Gannon *et al.* 2018). The *Limulus* amebocyte lysate (LAL) test has become the method of choice to test for pathogens in injectable drugs, vaccines, and implantable medical devices (Smith *et al.* 2017; Krisfalusi-Gannon *et al.* 2018). Blood from horseshoe crabs for LAL production is obtained by collecting adult crabs, extracting a portion of their blood (<40% of blood volume), and releasing them alive (Smith *et al.* 2017). Short-term mortality from bleeding is estimated to be 15% (4 to 30%) while a long-term study showed no significant effect on mortality (Smith *et al.* 2017; 2020). A different situation occurs in south east Asia where horseshoe crabs are killed in the process of extracting blood (John *et al.* 2018).

## Other Spider Crabs

Other spider crab species (Family Majidae) are known to show aggregating behaviour, but apparently not to the spectacular extent shown by the giant spider crab in southern Australia. The spider crab *Libinia emarginata* occurs along the Atlantic coast of North America, and has been observed forming large pods when moulting in the northern fall, as well as aggregating for spawning in the northern spring, and overwintering in deep water in aggregations (Degoursey and Auster 1992). On the Atlantic coast of Spain, the spider crab *Maja squinado* forms aggregations in shallow coastal waters (Sampedro and González-Gurriarán 2004; Corgos *et al.* 2010). “Pods” of spider crabs formed in September to November, and were mostly comprised of juveniles although in some cases adults were also present

(Sampedro and González-Gurriarán 2004). The timing of the aggregations coincided with the annual peak in moulting and Sampedro and González-Gurriarán (2004) suggested that the aggregation behaviour most likely functioned to protect the moulting crabs from predators. Pods in shallow water are not thought to be linked to reproduction because mating is thought to occur in the intermoult stage in deep water and the spawning period is over the summer months (Freire *et al.* 2002; Sampedro and González-Gurriarán 2004).

## **Discussion**

As shown in this review, spectacular aggregations can occur in diverse marine invertebrate groups. Of the marine invertebrate aggregations covered in this review, a significant proportion occur in Australian waters. While most of the invertebrate aggregations reviewed here are of high value for tourism and recreational diving, many are also valued as fishing species. As such, managing the sustainability of these aggregations must take into account a range of stakeholder interests and points of view.

If localised and predictable in time and place, aggregations of marine animals can be vulnerable to overfishing, because less search effort is required of fishers to achieve large catches (Sadovy de Mitcheson and Erisman 2012). Managing the fishing of aggregations can be complicated by “hyperstability”, where catch rates from the aggregation can remain stable even as the population declines (Erisman *et al.* 2011). In this review, rapidly increasing catches and associated population declines occurred in relation to aggregations of giant Australian cuttlefish, ornate rock lobster, and horseshoe crabs. Management tools that were applied included spatial closures (seasonal or total) to fishing methods to which the species were most vulnerable (e.g. jigs for giant cuttlefish, trawling for ornate rock lobster). Input and output controls to limit catches based on fishery assessments have also been applied (giant cuttlefish, ornate rock lobster, horseshoe crabs). In one case, the declaration of a marine protected area acted as a management tool to reduce fishing pressure (horseshoe crabs). In an extreme case the decline in the population of giant cuttlefish in the 2000’s led to the closure of the entire commercial fishery. Application of these management tools has generally been successful, with sustainable populations currently observed in these species. Management is complicated by the fact that populations of marine invertebrates, especially those that are fast growing and have short generation times (e.g. cuttlefish, calamari and jellyfish), can show major population fluctuations in relation to environmental changes.

Management for sustainability of invertebrate aggregations has generally been underpinned by comprehensive scientific research and a detailed understanding of the species’ life history (giant cuttlefish, ornate rock lobster, Christmas Island red crab, North Atlantic horseshoe crabs). Management has also included fishery-independent monitoring to track the population trajectory of aggregating invertebrate species. Monitoring programs need to be carefully designed to take the highly aggregated distribution of individuals into account when estimating population size. Because there is great public interest in these spectacular aggregations, researchers have been able to enlist the help of citizen science networks to conduct the monitoring. Citizen science monitoring has been increasing internationally (Conrad and Hilchey 2011; Tulloch *et al.* 2013) and has the benefit of cost-effectiveness and contributing to public education and support (Conrad and Hilchey 2011). Citizen scientists can make increased spatial and temporal coverage of sampling possible (Bonney *et al.* 2009; Tulloch *et al.* 2013), for example, 100’s of volunteers undertake simultaneous coverage of dozens of beaches throughout Delaware Bay for horseshoe crab monitoring (Smith and Michels 2006). Well-designed surveys conducted by citizen scientists can be an effective investment for measuring management impacts (Tulloch *et al.* 2013). Such programs, however, need to ensure that volunteers are properly trained and that there is adequate quality control of the data collected (Conrad and Hilchey 2011).



Management of marine invertebrate aggregations has typically involved advisory committees based on a diverse range of stakeholders including government agencies, researchers, industry (fishing, recreational diving, tourism) and conservation organisations. In the case of the Delaware Bay Horseshoe crab aggregation, stakeholder input and consensus is part of an adaptive management framework (Pratt Miles 2013) where management actions are implemented based on a chosen harvest strategy and then reviewed and, if necessary, modified on a periodic basis (McGowan *et al.* 2011; McGowan *et al.* 2015). Invertebrate aggregations are conspicuous features of the ecosystem and can have a significant impact on other ecosystem components, for example the interaction between horseshoe crabs and migratory shorebirds, and between Christmas Island red crabs and the annual whale shark aggregation. Aggregations can also be impacted by other ecosystem components, for example the impact of yellow crazy ants on Christmas Island red crabs. In this case the implementation of ecosystem based management is preferable to management based on a single species (Tan and Jardine 2019).

Invertebrate aggregations can have major economic non-fishing benefits. For example, the red land crabs are the major tourist attraction on Christmas Island and golden jellyfish are the major tourist attraction on the Palau archipelago and are also a major attraction in Raja Ampat, Indonesia. This tourism forms part of the strong growth in coastal tourism (Hall 2001) that can contribute significantly to local economies (Tapsuwan and Asafu-Adjaye 2008; Stoeckl *et al.* 2010). Detailed assessments of the non-fishing economic benefits of marine invertebrate aggregations are generally lacking, although an assessment has been done on the tourism value of the horseshoe crab / migratory shorebird aggregation in Delaware Bay (Edwards *et al.* 2011), and this type of analysis could be undertaken for other aggregations. Good examples of this type of analysis have been undertaken for shark diving tourism. In the Maldives, the annual income from shark diving for the tourism industry was estimated to be US \$154.83 million, and analysis indicated that increased shark conservation could raise this figure significantly (Zimmerhackel *et al.* 2018). In an example of a marine aggregation in Australia, the whale shark diving tourism in the Ningaloo Region of Western Australia was estimated to annually generate AUD \$11.59 million in expenditure directly benefiting diving operators and a further AUD \$12.55 million annual expenditure in the region related to the shark diving tourism (Huveneers *et al.* 2017).

The social benefits that can be associated with marine invertebrate aggregations are also significant. As well as economic benefits, coastal tourism and recreation can lead to increased “social capital” (Pretty and Smith 2004) where community awareness and understanding of the invertebrate aggregations and associated management and conservation is increased. For example, local initiatives such as the annual “Cuttlefest” in Whyalla can help to increase tourism and associated economic benefits, and at the same time can build social capital. Invertebrate aggregations can also stimulate significant education and learning experiences, with a number of learning centres and museums focussed on aggregations reviewed here. Finally, invertebrate aggregations can have significant social and cultural value for artisanal fishers. For example, the traditional fishery for ornate rock lobsters has significant social and cultural value for the Torres Strait Islander community, and consideration of these values has been incorporated into management plans through strong stakeholder involvement in plan development.

In summary, significant information is available on the management of marine invertebrate aggregations that will inform the appropriate management of the Australian giant spider crab. Management tools that have been used in species subject to fishing include seasonal or permanent closure of the aggregation area to specific fishing methods, restrictions on catch, and inclusion in marine protected areas. Management has been underpinned by a detailed understanding of the species’ life history as well as population monitoring, often facilitated by citizen scientists. Stakeholder input has



been an important factor in the development of management strategies for aggregating species. Economic (non-fishing) value of aggregations to local communities can be high but has seldom been measured in detail. Aggregations can also have high social and cultural value, with the building of “social capital” contributing to community understanding and support of conservation and management of aggregating populations.

## References

- Adamczewska, A. M., and Morris, S. (2001). Ecology and behavior of *Gecarcoidea natalis*, the Christmas Island red crab, during the annual breeding migration. *Biological Bulletin* **200**, 305-320. doi:<https://doi.org/10.2307/1543512>
- Anon. (2012). Upper Spencer Gulf Marine Park Management Plan 2012. Department of Environment, Water and Natural Resources, Government of South Australia.
- Anon. (2016). 'The famous jellyfish lake is running out of jellyfish.' Available at <https://www.nationalgeographic.com/animals/article/160504-golden-jellyfish-disappear-from-palau-lake>.
- Anon. (2019a). 'The Story of the Bigfin Reef Squid.' Available at <https://muroto-taikan.jp/english/a05b02.html>.
- Anon. (2019b). 'Tourists return to bathe with Palau's golden jellyfish.' Available at <https://www.phnompenhpost.com/travel/tourists-return-bathe-palaus-golden-jellyfish>.
- Anon. (2020a). 'Cuttlefish population survey.' Available at [https://www.pir.sa.gov.au/fishing/recreational\\_fishing/cuttlefish/population\\_survey](https://www.pir.sa.gov.au/fishing/recreational_fishing/cuttlefish/population_survey).
- Anon. (2020b). 'Giant Australian Cuttlefish.' Available at [https://www.pir.sa.gov.au/fishing/recreational\\_fishing/cuttlefish](https://www.pir.sa.gov.au/fishing/recreational_fishing/cuttlefish).
- Anon. (2020c). 'Whyalla's 2020 Cuttlefest.' Available at <https://www.whyalla.com/cuttlefest>.
- Anon. (2021). 'Christmas Island Red Crab Migration.' Available at <https://www.christmas.net.au/experiences/red-crab-migration/>.
- Baumgartner, N. R., and Ryan, S. D. (2020). Interaction of red crabs with yellow crazy ants during migration on Christmas Island. *Mathematical Biosciences* **330**, 108486. doi:<https://doi.org/10.1016/j.mbs.2020.108486>
- Bonney, R., Cooper, C. B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K. V., and Shirk, J. (2009). Citizen science: A developing tool for expanding science knowledge and scientific literacy. *Bioscience* **59**, 977-984. doi:<https://doi.org/10.1525/bio.2009.59.11.9>
- Chen, C.-S., Chen, J.-Y., and Lin, C.-W. (2015). Variation in life-history traits for micro-cohorts of *Sepioteuthis lessoniana* in the waters off northern Taiwan. *Fisheries Science* **81**, 53-64. doi:<https://doi.org/10.1007/s12562-014-0831-x>
- Chen, T.-C., Ku, K.-C., and Chen, C.-S. (2016). Collaborative adaptive management for bigfin squid applied to tourism-related activities in coastal waters of Northeast Taiwan. *Ocean and Coastal Management* **119**, 208-216. doi:<https://doi.org/10.1016/j.ocecoaman.2015.10.010>
- Chiang, C.-I., Chung, M.-T., Shiao, J.-C., Wang, P.-L., Chan, T.-Y., Yamaguchi, A., and Wang, C.-H. (2020). Seasonal movement patterns of the bigfin reef squid *Sepioteuthis lessoniana* predicted using statolith  $\delta^{18}\text{O}$  values. *Frontiers in Marine Science* **7**, 249. doi:<https://doi.org/10.3389/fmars.2020.00249>

- Ching, T.-Y., Chen, C.-S., and Wang, C.-H. (2019). Spatiotemporal variations in life-history traits and statolith trace elements of *Sepioteuthis lessoniana* populations around northern Taiwan. *Journal of the Marine Biological Association of the United Kingdom* **99**, 203-213.  
doi:<https://doi.org/10.1017/S0025315417001801>
- Conrad, C. C., and Hilchey, K. G. (2011). A review of citizen science and community-based environmental monitoring: issues and opportunities. *Environmental Monitoring and Assessment* **176**, 273-291. doi:<https://doi.org/10.1007/s10661-010-1582-5>
- Corgos, A., Sanchez, N., and Freire, J. (2010). Dynamics of the small-scale spatial structure of a population of the spider crab *Maja brachydactyla* (Decapoda: Majidae). *Journal of Shellfish Research* **29**, 25-36.
- Dawson, M. N., Martin, L. E., and Penland, L. K. (2001). Jellyfish swarms, tourists, and the Christ-child. *Hydrobiologia* **451**, 131-144. doi:<https://doi.org/10.1023/A:1011868925383>
- Degoursey, R. E., and Auster, P. J. (1992). A mating aggregation of the spider crab (*Libinia emarginata*). *Journal of Northwest Atlantic Fishery Science* **13**, 77-82.  
doi:<https://doi.org/10.2960/J.v13.a6>
- Dennis, D. M., Pitcher, C. R., Prescott, J. H., and Skewes, T. D. (1992). Severe mortality in a breeding population of ornate rock lobster *Panulirus ornatus* (Fabricius) at Yule Island, Papua New Guinea. *Journal of Experimental Marine Biology and Ecology* **162**, 143-158.  
doi:[https://doi.org/10.1016/0022-0981\(92\)90198-J](https://doi.org/10.1016/0022-0981(92)90198-J)
- Dennis, D. M., Pitcher, C. R., and Skewes, T. D. (2002). Distribution and transport pathways of *Panulirus ornatus* (Fabricius, 1776) and *Panulirus* spp. larvae in the Coral Sea, Australia. *Marine and Freshwater Research* **52**, 1175-1185. doi:<https://doi.org/10.1071/MF01186>
- Edwards, P. E. T., Parsons, G. R., and Myers, K. H. (2011). The economic value of viewing migratory shorebirds on the Delaware Bay: An application of the single site travel cost model using on-site data. *Human Dimensions of Wildlife* **16**, 435-444.  
doi:<https://doi.org/10.1080/10871209.2011.608180>
- Ehlinger, G. S., Tankersley, R. A., and Bush, M. B. (2003). Spatial and temporal patterns of spawning and larval hatching by the horseshoe crab, *Limulus polyphemus*, in a microtidal coastal lagoon. *Estuaries* **26**, 631-640.
- Erismann, B. E., Allen, L. G., Claisse, J. T., Pondella, D. J., Miller, E. F., and Murray, J. H. (2011). The illusion of plenty: Hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 1705-1716.  
doi:<https://doi.org/10.1139/f2011-090>
- Freire, J., Bernárdez, C., Corgos, A., Fernández, L., González-Gurriarán, E., Sampedro, M. P., and Verísimo, P. (2002). Management strategies for sustainable invertebrate fisheries in coastal ecosystems of Galicia (NW Spain). *Aquatic Ecology* **36**, 41-50.  
doi:<https://doi.org/10.1023/A:1013350723445>
- Green, P. T., O'Dowd, D. J., and Lake, P. S. (1997). Control of seedling recruitment by land crabs in rain forest on a remote oceanic island. *Ecology* **78**, 2474-2486.  
doi:[https://doi.org/10.1890/0012-9658\(1997\)078\[2474:COSRBL\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[2474:COSRBL]2.0.CO;2)

- Green, P. T., O'Dowd, D. J., and Lake, P. S. (2008). Recruitment dynamics in a rainforest seedling community: context-independent impact of a keystone consumer. *Oecologia* **156**, 373-385. doi:<https://doi.org/10.1007/s00442-008-0992-3>
- Hall, C. M. (2001). Trends in ocean and coastal tourism: the end of the last frontier? *Ocean & Coastal Management* **44**, 601-618. doi:[https://doi.org/10.1016/S0964-5691\(01\)00071-0](https://doi.org/10.1016/S0964-5691(01)00071-0)
- Hall, K., and Hanlon, R. (2002). Principal features of the mating system of a large spawning aggregation of the giant Australian cuttlefish *Sepia apama* (Mollusca: Cephalopoda). *Marine Biology* **140**, 533-545. doi:<https://doi.org/10.1007/s00227-001-0718-0>
- Hall, K. C., Fowler, A. J., and Geddes, M. C. (2007). Evidence for multiple year classes of the giant Australian cuttlefish *Sepia apama* in northern Spencer Gulf, South Australia. *Reviews in Fish Biology and Fisheries* **17**, 367. doi:<https://doi.org/10.1007/s11160-007-9045-y>
- Hall, K. C., Fowler, A. J., Geddes, M. C., and Taylor, J. D. (2018). Predictable spatiotemporal dynamics of a dense cuttlefish spawning aggregation increases its vulnerability to exploitation. *ICES Journal of Marine Science* **75**, 221-234. doi:<https://doi.org/10.1093/icesjms/fsx099>
- Hanlon, R. T., Naud, M. J., Shaw, P. W., and Havenhand, J. N. (2005). Behavioural ecology: Transient sexual mimicry leads to fertilization. *Nature* **433**, 212. doi:<https://doi.org/10.1038/433212a>
- Hicks, J. W. (1985). The breeding behaviour and migrations of the terrestrial crab *Gecarcoidea natalis* (Decapoda: Brachyura). *Australian Journal of Zoology* **33**, 101-110. doi:<https://doi.org/10.1071/ZO9850127>
- Hutton, T., van Putten, E. I., Pascoe, S. D., Deng, R. A., Plagányi, É. E., and Dennis, D. (2016). Trade-offs in transitions between indigenous and commercial fishing sectors: the Torres Strait tropical rock lobster fishery. *Fisheries Management and Ecology* **23**, 463-477. doi:<https://doi.org/10.1111/fme.12186>
- Huveneers, C., Meekan, M. G., Apps, K., Ferreira, L. C., Pannell, D., and Vianna, G. M. S. (2017). The economic value of shark-diving tourism in Australia. *Reviews in Fish Biology and Fisheries* **27**, 665-680. doi:<https://doi.org/10.1007/s11160-017-9486-x>
- John, B. A., et al. (2018). A review on fisheries and conservation status of Asian horseshoe crabs. *Biodiversity and Conservation* **27**, 3573-3598. doi:<https://doi.org/10.1007/s10531-018-1633-8>
- Kennelly, S. J., and Broadhurst, M. K. (2014). Mitigating the bycatch of giant cuttlefish *Sepia apama* and blue swimmer crabs *Portunus armatus* in an Australian penaeid-trawl fishery. *Endangered Species Research* **26**, 161-166. doi:<https://doi.org/10.3354/esr00639>
- Krisfalusi-Gannon, J., et al. (2018). The role of horseshoe crabs in the biomedical industry and recent trends impacting species sustainability. *Frontiers in Marine Science* **5**, 185. doi:<http://dx.doi.org/10.3389/fmars.2018.00185>
- Landi, A. A., Vokoun, J. C., Howell, P., and Auster, P. (2015). Predicting use of habitat patches by spawning horseshoe crabs (*Limulus polyphemus*) along a complex coastline with field surveys and geospatial analyses. *Aquatic Conservation: Marine and Freshwater Ecosystems* **25**, 380-395. doi:<https://doi.org/10.1002/aqc.2440>

- Lin, C.-Y., and Chiao, C.-C. (2017). Female choice leads to a switch in oval squid male mating tactics. *The Biological Bulletin* **233**, 219-226. doi:<https://doi.org/10.1086/695718>
- Lin, C.-Y., Tsai, Y.-C., and Chiao, C.-C. (2017). Quantitative analysis of dynamic body patterning reveals the grammar of visual signals during the reproductive behavior of the oval squid *Sepioteuthis lessoniana*. *Frontiers in Ecology and Evolution* **5**, 30. doi:<https://doi.org/10.3389/fevo.2017.00030>
- Maas, D. L., *et al.* (2020). Recognizing peripheral ecosystems in marine protected areas: A case study of golden jellyfish lakes in Raja Ampat, Indonesia. *Marine Pollution Bulletin* **151**, 110700. doi:<https://doi.org/10.1016/j.marpolbul.2019.110700>
- MacFarlane, J., and Moore, R. (1986). Reproduction of the ornate rock lobster, *Panulirus ornatus* (Fabricius), in Papua New Guinea. *Marine and Freshwater Research* **37**, 55-65. doi:<https://doi.org/10.1071/MF9860055>
- McGowan, C. P., *et al.* (2015). Implementation of a framework for multi-species, multi-objective adaptive management in Delaware Bay. *Biological Conservation* **191**, 759-769. doi:<https://doi.org/10.1016/j.biocon.2015.08.038>
- McGowan, C. P., *et al.* (2011). Multispecies modeling for adaptive management of horseshoe crabs and red knots in the Delaware bay. *Natural Resource Modeling* **24**, 117-156. doi:<https://doi.org/10.1111/j.1939-7445.2010.00085.x>
- Meekan, M. G., Jarman, S. N., McLean, C., and Schultz, M. B. (2009). DNA evidence of whale sharks (*Rhincodon typus*) feeding on red crab (*Gecarcoidea natalis*) larvae at Christmas Island, Australia. *Marine and Freshwater Research* **60**, 607-609. doi:<https://doi.org/10.1071/MF08254>
- Moore, R., and MacFarlane, J. (1984). Migration of the Ornate Rock Lobster, *Panulirus ornatus* (Fabricius), in Papua New Guinea. *Marine and Freshwater Research* **35**, 197-212. doi:<https://doi.org/10.1071/MF9840197>
- Myers, K. H., Parsons, G. R., and Edwards, P. E. T. (2010). Measuring the recreational use value of migratory shorebirds on the Delaware Bay. *Marine Resource Economics* **25**, 247-264. doi:<https://doi.org/10.5950/0738-1360-25.3.247>
- Noell, C. J., Broadhurst, M. K., and Kennelly, S. J. (2018). Refining a Nordmøre-grid bycatch reduction device for the Spencer Gulf penaeid-trawl fishery. *PLoS ONE* **13**, e0207117. doi:<https://doi.org/10.1371/journal.pone.0207117>
- Norman, M. D., Finn, J., and Tregenza, T. (1999). Female impersonation as an alternative reproductive strategy in giant cuttlefish. *Proceedings of the Royal Society B: Biological Sciences* **266**, 1347-1349. doi:<https://doi.org/10.1098/rspb.1999.0786>
- O'Dowd, D. J., Green, P. T., and Lake, P. S. (2003). Invasional 'meltdown' on an oceanic island. *Ecology Letters* **6**, 812-817. doi:<https://doi.org/10.1046/j.1461-0248.2003.00512.x>
- O'Dowd, D. J., and Lake, P. S. (1989). Red crabs in rain forest, Christmas Island: Removal and relocation of leaf-fall. *Journal of Tropical Ecology* **5**, 337-348. doi:<https://doi.org/10.1017/S0266467400003746>

- O'Dowd, D. J., and Lake, P. S. (1990). Red crabs in rain forest, Christmas Island: differential herbivory of seedlings. *Oikos* **58**, 289-292. doi:<https://doi.org/10.2307/3545219>
- O'Dowd, D. J., and Lake, P. S. (1991). Red crabs in rain forest, Christmas Island: Removal and fate of fruits and seeds. *Journal of Tropical Ecology* **7**, 113-122. doi:<https://doi.org/10.1017/S0266467400005162>
- Pecl, G. (2001). Flexible reproductive strategies in tropical and temperate *Sepioteuthis* squids. *Marine Biology* **138**, 93-101. doi:<https://doi.org/10.1007/s002270000452>
- Pitcher, C. R., Dennis, D. M., and Skewes, T. D. (1997). Fishery-independent surveys and stock assessment of *Panulirus ornatus* in Torres Strait. *Marine and Freshwater Research* **48**, 1059-1067. doi:<https://doi.org/10.1071/MF97199>
- Pitcher, C. R., Skewes, T. D., Dennis, D. M., and Prescott, J. H. (1992). Estimation of the abundance of the tropical lobster *Panulirus ornatus* in Torres Strait, using visual transect-survey methods. *Marine Biology* **113**, 57-64. doi:<https://doi.org/10.1007/BF00367638>
- Plagányi, É. E., *et al.* (2018). Overview, opportunities and outlook for Australian spiny lobster fisheries. *Reviews in Fish Biology and Fisheries* **28**, 57-87. doi:<https://doi.org/10.1007/s11160-017-9493-y>
- Plagányi, É. E., *et al.* (2013). Integrating indigenous livelihood and lifestyle objectives in managing a natural resource. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 3639-3644.
- Pratt Miles, J. D. (2013). Designing collaborative processes for adaptive management: Four structures for multistakeholder collaboration. *Ecology and Society* **18**, 5. doi:<https://doi.org/10.5751/ES-05709-180405>
- Pretty, J., and Smith, D. (2004). Social capital in biodiversity conservation and management. *Conservation Biology* **18**, 631-638.
- Prowse, T. A. A., *et al.* (2015). Evidence for a broad-scale decline in giant Australian cuttlefish *Sepia apama* abundance from non-targeted survey data. *Marine and Freshwater Research* **66**, 692-700. doi:<https://doi.org/10.1071/MF14081>
- Sadovy de Mitcheson, Y., and Erisman, B. (2012). Fishery and Biological Implications of Fishing Spawning Aggregations, and the Social and Economic Importance of Aggregating Fishes. In 'Reef Fish Spawning Aggregations: Biology, Research and Management'. (Eds Y. Sadovy de Mitcheson and P. L. Colin.) pp. 225-284. (Springer Netherlands: Dordrecht.)
- Sampedro, M.-P., and González-Gurriarán, E. (2004). Aggregating behaviour of the spider crab *Maja squinado* in shallow waters. *Journal of Crustacean Biology* **24**, 168-177.
- Schnell, A. K., Smith, C. L., Hanlon, R. T., Hall, K. C., and Harcourt, R. (2016). Cuttlefish perform multiple agonistic displays to communicate a hierarchy of threats. *Behavioral Ecology and Sociobiology* **70**, 1643-1655. doi:<https://doi.org/10.1007/s00265-016-2170-7>
- Skewes, T. D., Pitcher, R. C., and Trendall, J. T. (1994). Changes in the size structure, sex ratio and molting activity of a population of ornate rock lobsters, *Panulirus ornatus*, caused by an annual maturation molt and migration. *Bulletin of Marine Science* **54**, 38-48.



- Smith, D. R., Brockmann, H. J., Beekey, M. A., King, T. L., Millard, M. J., and Zaldívar-Rae, J. (2017). Conservation status of the American horseshoe crab, (*Limulus polyphemus*): a regional assessment. *Reviews in Fish Biology and Fisheries* **27**, 135-175. doi:<https://doi.org/10.1007/s11160-016-9461-y>
- Smith, D. R., and Michels, S. F. (2006). Seeing the Elephant. *Fisheries* **31**, 485-491. doi:[https://doi.org/10.1577/1548-8446\(2006\)31\[485:STE\]2.0.CO;2](https://doi.org/10.1577/1548-8446(2006)31[485:STE]2.0.CO;2)
- Smith, D. R., Newhard, J. J., McGowan, C. P., and Butler, C. A. (2020). The long-term effect of bleeding for *Limulus* amebocyte lysate on annual survival and recapture of tagged horseshoe crabs. *Frontiers in Marine Science* **7**, 607668. doi:<http://dx.doi.org/10.3389/fmars.2020.607668>
- Smith, D. R., and Robinson, T. J. (2015). Horseshoe crab spawning activity in delaware bay, USA, after harvest reduction: A mixed-model analysis. *Estuaries and Coasts* **38**, 2345-2354. doi:<https://doi.org/10.1007/s12237-015-9961-3>
- Steer, M. A., Gaylard, S., and Loo, M. (2013). Monitoring the relative abundance and biomass of South Australia's Giant Cuttlefish breeding population. Final Report for the Fisheries Research and Development Corporation. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2013/000074-1. SARDI Research Report Series No.684.103 pp.
- Steer, M. A., Matthews, D. J., and Gaylard, S. (2016). Giant Australian Cuttlefish (*Sepia apama*) surveys 1998 - 2015. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No.F 2015/000771-1. SARDI Research Report Series No. 886. 18 pp.
- Stoeckl, N., Birtles, A., Farr, M., Mangott, A., Curnock, M., and Valentine, P. (2010). Live-aboard dive boats in the great barrier reef: Regional economic impact and the relative values of their target marine species. *Tourism Economics* **16**, 995-1018. doi:<https://doi.org/10.5367/te.2010.0005>
- Sugimoto, C., and Ikeda, Y. (2012). Ontogeny of schooling behavior in the oval squid *Sepioteuthis lessoniana*. *Fisheries Science* **78**, 287-294. doi:<https://doi.org/10.1007/s12562-011-0464-2>
- Sugimoto, C., Yanagisawa, R., Nakajima, R., and Ikeda, Y. (2013). Observations of schooling behaviour in the oval squid *Sepioteuthis lessoniana* in coastal waters of Okinawa Island. *Marine Biodiversity Records* **6**, e34. doi:<https://doi.org/10.1017/S1755267213000067>
- Tan, Y., and Jardine, S. L. (2019). Considering economic efficiency in ecosystem-based management: The case of horseshoe crabs in Delaware Bay. *Environmental and Resource Economics* **72**, 511-538. doi:<https://doi.org/10.1007/s10640-017-0204-x>
- Tapsuwan, S., and Asafu-Adjaye, J. (2008). Estimating the Economic Benefit of SCUBA Diving in the Similan Islands, Thailand. *Coastal Management* **36**, 431-442. doi:<https://doi.org/10.1080/08920750802412908>
- Taylor, J., and Poore, G. (2017). 'Leptomithrax gaimardii Giant Spider Crab in Museums Victoria Collections.' Available at <https://collections.museumsvictoria.com.au/species/14370>.

- Tulloch, A. I. T., Possingham, H. P., Joseph, L. N., Szabo, J., and Martin, T. G. (2013). Realising the full potential of citizen science monitoring programs. *Biological Conservation* **165**, 128-138. doi:<https://doi.org/10.1016/j.biocon.2013.05.025>
- van Putten, I., Deng, R., Dennis, D., Hutton, T., Pascoe, S., Plagányi, E., and Skewes, T. (2013). The quandary of quota management in the Torres Strait rock lobster fishery. *Fisheries Management and Ecology* **20**, 326-337. doi:<https://doi.org/10.1111/fme.12015>
- VFA (2018). 'Giant Spider Crab Distribution and Biology.' Available at <https://vfa.vic.gov.au/science-in-fisheries/spidercrabs/giant-spider-crab-distribution-and-biology>.
- Ye, Y., and Dennis, D. (2009). Assessing the impacts of trawling breeding lobsters (*Panulirus ornatus*) on the catch of the Torres Strait lobster fishery shared between Australia and Papua New Guinea. *New Zealand Journal of Marine and Freshwater Research* **43**, 419-428. doi:<https://doi.org/10.1080/00288330909510011>
- Zimmerhackel, J. S., Rogers, A. A., Meekan, M. G., Ali, K., Pannell, D. J., and Kragt, M. E. (2018). How shark conservation in the Maldives affects demand for dive tourism. *Tourism Management* **69**, 263-271. doi:<https://doi.org/10.1016/j.tourman.2018.06.009>