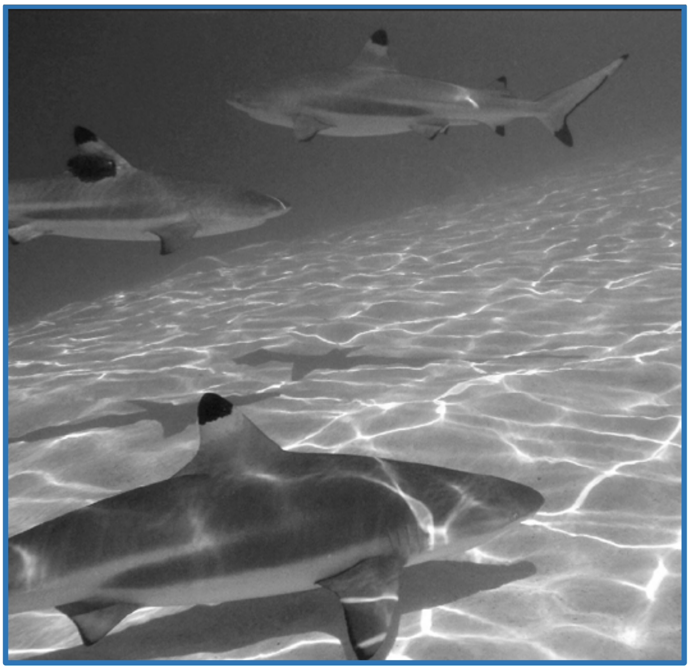

THE ECOLOGICAL ROLES OF SHARKS & RAYS IN MARINE ENVIRONMENTS

A scientific review and synthesis of
available knowledge and information

2019

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The ecological roles of sharks and rays in marine environments

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Suggested Citation

Chin, A. and Bierwagen, S. (2019), The ecological roles of sharks and rays in marine environments. Report to the World Wide Fund for Nature, *42 pages*.

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Technical terms

Apex predator: a species that once fully grown is positioned at the top of a food web and has no natural predators.

Ecological Role (ecological niche): species importance to an ecosystem based on functional and behavioral characteristics. The ecological role determines the effect a species has on a community/ecosystem, and what might happen if that species were removed.

Functional diversity: species with distinct functional traits in an ecosystem.

Functional redundancy: multiple species sharing similar functional traits in an ecosystem. High functional redundancy infers ecosystem resilience.

Functional role: species performance (e.g. predation) in an ecosystem based on organismal traits (e.g. diet, habitat use, tooth morphology).

Keystone species: species with specialised or unique traits that play a critical role in the ecosystem (e.g. they regulate habitats, populations and/or communities). Its impact on its community is much larger than would otherwise be expected from its abundance (Power and Scott Mills 1995).

Neonate: earliest stage of development and growth for newly hatched or born young.

Ontogeny: the change in habitat use and diet between juvenile and adult life stages.

Top predator: a species that once fully grown is positioned near the top of the food web, and has few natural predators.

Trophic cascade: a series of cascading ripple effects caused from removal of a species in an ecosystem.

Trophic ecology: field of study that determines what an animal eats and how energy flows through the ecosystem (encompasses diet and food webs).

EXECUTIVE SUMMARY

Sharks and rays are a very diverse group of animals with a wide range of body sizes, life history features and functional traits. This variation implies that sharks and rays have a wide range of ecological roles. There has been increasing interest in the ecological role of sharks and rays, especially due to concerns that declines in sharks and ray populations may cause serious cascading effects in marine ecosystems. Conservation narratives have stated that healthy shark populations are necessary to maintain healthy oceans. The scientific literature has offered some examples that healthy coral reefs have more sharks, but whether sharks contribute to maintaining reef health is a well-known debate among scientists.

This review was commissioned to provide a synthesis of the latest scientific information about the roles of sharks and rays in marine ecosystems, examining the concept of sharks and rays being keystone species that regulate marine ecosystems. The review was limited to published scientific accounts and sought to identify key case studies, and accounts of shark and ray ecological roles by specific habitats. Over 190 scientific papers were examined.

Most of the published scientific information on shark and ray ecological roles focuses on trophic ecology, that is, studies of the diet, energy flow and feeding habits of sharks and rays. This information is then often used to *infer* the species' ecological roles based on diet and ecological theory about predator-prey dynamics. In general, it is clear that sharks and rays have a wide range of diets that can change individuals grow from juveniles to adults. These feeding preferences even vary between populations in different locations. As a consequence, a species' ecological role can significantly change across time and space. For example, the trophic level and ecological roles of grey reef sharks can change between reefs and regions. This variability makes it difficult to form generic statements about ecological roles that can be widely applied across shark and ray species and habitats, and indeed, there is inconsistency and lack of consensus in scientific literature in the field.

Nevertheless, several case studies have emerged that illustrate the ecological roles of some sharks and rays. Apex predators such as tiger sharks can cause trophic cascades in coastal seagrass systems by altering prey behavior, leading to increased seagrass density. The presence of reef sharks can also alter prey behavior of herbivores, although the wider ecosystem effects of these changes are unclear. Stingrays can act as habitat engineers, creating microhabitats and turning over sediments as they feed. Their feeding activities can also facilitate foraging for other species. Sharks and rays can also transfer energy between ecosystems. For example, grey reef sharks bring nutrients from pelagic ecosystems to coral reef ecosystems and Chilean devil rays transfer energy from the deep ocean to shallow waters. Nutrient cycling is an important oceanic process, where nutrient depleted areas can be supplemented by distribution between habitats via mobile species.

This review also includes habitat-specific examples of the current understanding of elasmobranch ecological roles:

> Most reef dwelling sharks and rays are mesopredators and they can have effects on coral reef communities, however these effects are highly variable and inconsistent between locations. Additionally, it should not be assumed that there are high levels of functional redundancy between reef predators, i.e. one should not assume that a blacktip reef shark can perform the same ecological role as a grey reef shark.
>
> Coastal habitats are complex and diverse, with a wide range of shark and ray species. These sharks and rays show a very wide diversity of diet and habitat use and thus, presumably a wide range of ecological roles. There is little available data to suggest that these species play strong ecological roles in coastal ecosystems, however these systems are extremely complex and detecting these patterns is challenging. There is also evidence of behavior mediated trophic cascades in specific locations.
>
> Deep water habitats are very poorly understood. Information on ecological roles is mainly based on trophic ecology of sharks and rays captured in fisheries which shows that teleost fishes and cephalopods are major prey items. While a few deep water sharks may function as apex predators (e.g. cowsharks), the ecological roles of most other species are largely unknown.
>
> There is limited evidence that pelagic sharks play important top-down effects in pelagic ecosystems. Nevertheless, it is difficult to study the trophic ecology of the large, highly mobile species in the open ocean. It should also be remembered that many pelagic shark and fish populations are depleted which complicates efforts to understand ecological relationships.

The review also found ample evidence to suggest that most sharks and rays are mesopredators, and that very few species act as apex predators. Additionally, no strong evidence was found for sharks or rays being keystone species, and there is limited direct evidence showing clear predator mediated trophic cascades. Indeed, most examples presented involve *inferences* made from trophic ecology or comparisons of fish and benthic communities between pristine reefs (where sharks are abundant) and impacted reefs (where sharks are depleted). Additionally, ecosystem models are often compromised by incomplete data, especially as basic dietary information is still lacking for many species.

The review also founds that far less is known about the ecological role of batoids than sharks, which is a concern given the growing concerns about the state of batoid populations. It should also be noted that much is still unknown about the trophic ecology and ecological roles of both sharks and rays, and foundational information such as comprehensive dietary information is still lacking for many species.

These limitations of the available data also highlight the possibility that sharks and rays may play key roles in marine ecosystems that are as yet, unknown. As such, the potential for ecological 'shocks and surprises' following the depletion of sharks and rays should not be underestimated.

The case studies and summative statements identified in this review provide opportunities to deliver clear examples of the potential ecological roles sharks and rays play in marine ecosystems. However, messages should be explicit about the species and locations involved to reduce ambiguity, and all messages should be framed within the appropriate context of species, life history stage, and location.

INTRODUCTION

There has been long-standing interest in the ecological roles predators play in marine ecosystems, especially given concerns that removing top predators could cause far reaching disruptions to marine ecosystems. The theoretical basis for these potential ecological effects and trophic cascades is well established, and indeed, these linkages have been widely documented in terrestrial ecosystems where removal (and reintroduction) of top predators such as wolves, leopards and lions have had significant flow-on effects (Ripple *et al.* 2014). However, there is still uncertainty and ongoing debate about the ecological roles predators such as sharks and rays play in marine ecosystems, and even uncertainty about the position of sharks and rays in trophic systems (Roff *et al.* 2016b; Ruppert *et al.* 2016). Meanwhile, there is a widespread conservation narrative that ocean predators such as sharks need to be conserved to maintain healthy ocean ecosystems. At the same time, new research is increasing scientific understanding about the trophic positioning and ecological roles of sharks and rays in the worlds' oceans.

This report presents a focused review of the available scientific literature concerning the trophic ecology and ecological roles of sharks and rays in marine environments. Specifically, this review examines what is known about shark and ray ecology and seeks to locate and assess studies that illustrate how declines in sharks and rays may affect ocean functioning and health. The review will cover major marine ecosystems and present several case studies regarding the potential effects sharks and rays have on marine ecosystems, and examine the extent of scientific evidence and consensus available regarding the importance of sharks and rays in maintaining ocean health and function.

Shark and ray diversity

There are approximately 1,250 extant species of sharks and rays present in the worlds' oceans, in a wide range of habitats ranging from deep ocean abyssal habitats to rivers and estuaries, and inland rivers and lakes, and across tropical to polar climates (Last *et al.* 2016). Their use of such a wide range of habitats and environmental regimes is reflected in the diversity of body size, form, and biology. For example, the diversity of chondrichthyan (sharks, skates and chimaeras) reproductive strategies far surpasses that of the teleost (bony) fishes. Similarly, sharks and rays have an extremely wide range of body forms. At 12 m total length, the whale shark (*Rhincodon typus*) is the worlds' largest shark (and largest fish), while the pygmy shark (*Euprotomicrus bispinatus*) only grows to 27 cm (Last and Stevens 2009). In comparative terms, a fully grown pygmy shark is only 0.0022 times the size of a whale shark. Thus, while all sharks and rays are predators, their diversity in size, form, and habitat use mean that the trophic ecology of sharks and rays, and the ecological roles they play, vary widely between species.

Individual size, age, and habitat use can also be a confounding factor within a single species. Neonate (new born) and juvenile sharks and rays are much smaller than their adult counterparts, and thus may be eaten by adults of the same species, driving smaller sharks to use discrete nursery habitats (Heupel *et al.* 2007; Heupel and Simpfendorfer 2011). However, as these small sharks grow larger, they may move into different habitats and their diet may also change (Chin *et al.* 2013). These ontognetic changes mean that a sharks' preferred prey, trophic position, and overall ecological role will change throughout its life cycle (Heupel *et al.* 2014). For example, a juvenile great hammerhead shark (*Sphyrna mokarran*) could be considered as prey to an adult blacktip reef shark (*Carcharhinus melanopterus*), however at 4.5 m long, a fully grown great hammerhead shark could hunt and consume an adult blacktip reef shark and other reef sharks (Mourier *et al.* 2013).

The conservation context

Sharks and rays are of conservation concern around the world with documented declines in numerous populations, and up to ¼ of extant shark and ray species currently considered as being at risk to extinction (Dulvy *et al.* 2014). The main threat is unsustainable fishing (e.g. Nadon *et al.* 2012), although habitat loss and degradation, environmental disturbances, and climate change also cause impacts (Chin *et al.* 2010; Dulvy *et al.* 2014), and can pose significant threats to some species such as river sharks (*Glyphis spp.*) and sawfishes (Morgan *et al.* 2011; Dulvy *et al.* 2014; Dulvy *et al.* 2017). These declines are also caused in part by the life history of many sharks and rays which, compared to teleost fishes, are relatively slow growing, late to mature, and have few young (Cortés 2004).

Messaging on the importance of conserving sharks and rays typically includes their ecological roles in maintaining healthy marine ecosystems. The narrative often revolves around a logic argument that removing top predators such as sharks will cause trophic imbalances that result in the 'release' of prey species when then multiply without predation control. This increased abundance of prey species then exerts increased predation or grazing pressure on other parts of the food web, causing a 'ripple effect' that reverberates throughout the ecosystem and leads to undesirable consequences.

However, it should also be noted that more recently, shark and ray conservation is also being framed in terms of their importance as living resources for ecotourism (e.g. Vianna *et al.* 2012), and for their importance to fisheries and livelihoods (e.g. Vieira *et al.* 2017), and the culture and identity of many peoples and communities (e.g. Hylton *et al.* 2017). Thus, while shark conservation narratives often revolve around their ecological roles, other values are emerging as reasons for shark and ray conservation. Nevertheless, the importance of at least some sharks and rays as keystone species that regulate ecosystem regulators is well founded in ecological theory, reinforced by numerous examples from terrestrial ecosystems (e.g. Ripple *et al.* 2014).

CURRENT METHODOLOGIES: HOW WE ‘KNOW’ WHAT WE KNOW

Marine ecologists have been intrigued by the ecological roles of sharks and rays for many years. However, conducting research on this topic is fundamentally challenging. Sharks and rays are relatively large species which make laboratory based studies difficult. They are also highly mobile, highly diverse, and inhabit challenging environments which make field studies and ‘manipulative’ ecological experiments very difficult.

Nevertheless, there is a growing body of scientific literature on the subject. We conducted a scientific literature review using standard literature sources including Scopus™, Google Scholar™, and Web of Science™. Searches were conducting using combinations of key search terms “shark”; “stingray”, ‘batoid”; “trophic role”; “ecological role”, “trophic ecology”; and “ecosystem role”. The first 100 papers returned from each combination of search terms was investigated. Duplicates were removed. As the literature was examined, key papers cited in sourced literature were also sourced. These searches collated over 190 relevant scientific papers which were used for this review. The key references and case studies were drawn upon and used in this report.

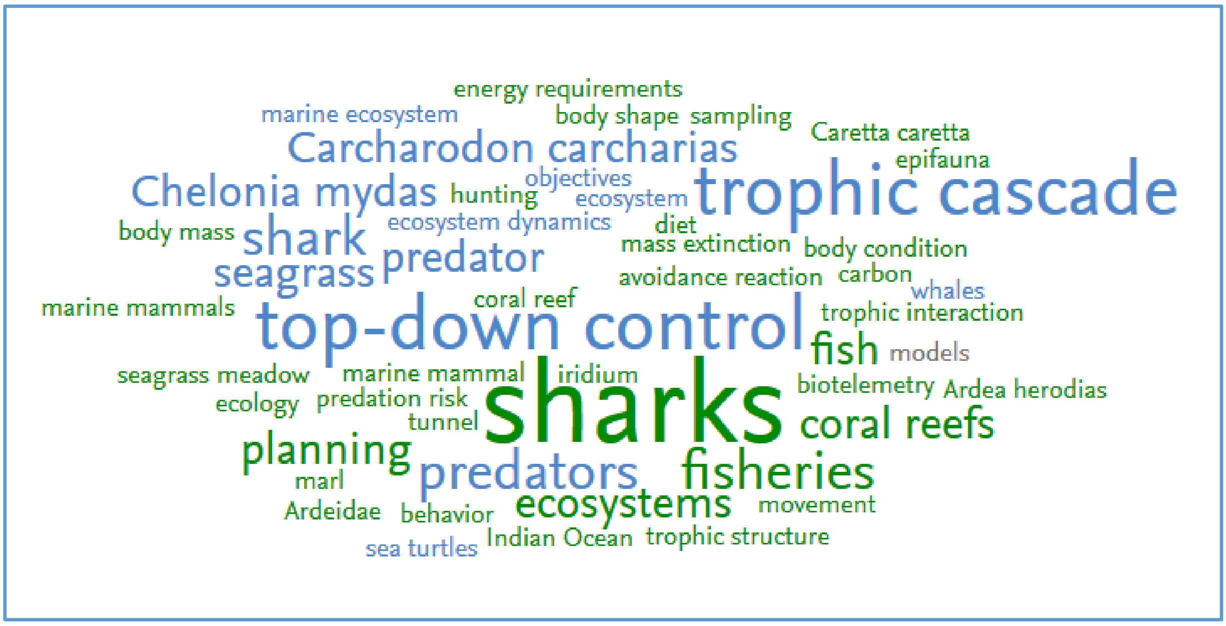


Fig. 1. A word cloud showing changing trends in scientific publications on shark and ray ecological role. It appears that research focus continues to grow and diversify, and understanding of the issue is evolving.

It should be noted that research in this area is constantly evolving. The ecological roles, and conservation ramifications of these roles, are a growing area of research interest. Fig 1 shows a key phrase word cloud produced by SciVal for papers from 2013-2018 for terms related to sharks and trophic cascades. The size of text shows the relevance to the search term and colour shows whether the number of publications in the area is growing (green) or declining (blue). As can been seen, there is growing interest in sharks, coral reefs, fisheries, and ecosystems, with declining studies on white sharks, top-down control, and trophic cascades. While these meta-analyses are relatively superficial, this example suggests that research in this area is expanding to include more species, and is exploring new and different areas of shark and ray ecology.

Essential terms and concepts

The scientific study of ecological roles is complex, and to avoid confusion and misinterpretation, it is essential that key terms are properly understood. An *ecological role* (sometimes referred to as ecological niche) is defined by how a species fits into an ecosystem, and the role it plays in that ecosystem. These roles are identified by describing the trait-based function (*functional role*) a species performs within a larger community or environment. Individual species have distinctive traits that can encompass characteristics such as diet, life-history, habitat use, genetic composition, morphology, and physiology, all of which contribute to how they function.

When multiple species in an ecosystem have different functional roles, they are considered to be functionally diverse. Alternatively, when multiple species carry the same functional role, they are considered functionally redundant. These distinctions are important in ecology since vulnerable species with unique functional roles may cause adverse effects to the ecosystem if they are depleted and no other species fills that role. For example, in coral reefs, the giant humphead parrotfish (*Bolbometopon muricatum*) performs a crucial role in bioerosion (Bellwood *et al.* 2003). While many parrotfishes act as bioeroders and thus share similar functional roles, the humphead is uniquely able to perform bioeroding functions over much larger areas due to its large body size. Without this particular species, ecosystem processes are disrupted. This complexity must be considered in our understanding of a species' ecological role. If research focuses only on species diversity and overlooks trait (functional) diversity to define ecosystem health, species with important ecological roles may be overlooked.

Importantly, functional roles do not always equate to ecological roles. A *functional role* describes a species' traits, whereas ecological roles describe how species traits influence the ecosystem. Thus, to completely understand a species' ecological role, its interactions with both the abiotic and biotic features of the ecosystem need to be understood. Furthermore, these interactions need to be considered within specific spatial and temporal contexts. Essentially, functional roles are related to species "*performance*" in an ecosystem, where ecological roles are related to species "*importance*" (Jax 2005). For these reasons, highly diverse and complex systems are hard to define at the functional level, which can lead to misunderstanding of species' ecological roles at the ecosystem level.

Key terms are clearly defined in the section "Technical Terms" on page 1.

Methods to determine ecological roles

Observation and inference

Some of the simplest accounts of the ecological roles or sharks and rays stem from direct observations of predation in the field. Due to the difficulty in gathering and quantifying the necessary information to describe ecological roles simultaneously, simplifications are often made to understand interactions that contribute to our understanding of ecology (Bierwagen *et al.* 2018). For example, SCUBA diver observations of wobbegong sharks (*Orectolobus* spp) preying upon other sharks can be used to infer trophic levels and hierarchies of different shark species (Ceccarelli and Williamson 2012). In general, direct observations are limited by the fact that (1) direct observations tend to be rare as observers have to be in 'the right place at the right time' to witness an event; and (2) it is difficult to determine how widespread and common the observed interaction is. This means that conclusions drawn from these observations are largely inferred due to the limited data.

Functional traits and diversity

Species' traits can be used to infer how characteristics of an organism contribute to its interactions with the environment. Traits are *"measurable features of an individual that potentially affects performance or fitness" (Cadotte et al. 2011)*. Physical traits include features which can be described such as physical appearance/composition (e.g. tooth morphology), biochemical such as physiological adaptations (e.g. thermal tolerance), behavioral (foraging modes), and time dependent variables (i.e. years to reach sexual maturity).

Examining these traits can help identify a species' possible *functional role* (e.g. how traits contribute to species performance). For example, a researcher may look at a specific trait such as jaw morphology and determine how that trait influences foraging behavior and diet. While this doesn't completely inform an ecological role, it gives insight to how a species may fit in a food web (e.g. trophic role/trophic level). More specifically in sharks, gape size (space available in a mouth) can limit the size of prey available for their diet (Lucifora *et al.* 2009). Defining these traits can help to create boundaries to understanding a species' overall function, but depending on the research focus, key aspects of how these play into ecosystem influence could remain unclear. For instance, describing gape traits will allow a researcher to understand what a species could potentially eat, but provides no information about the species' actual diet, highlighting the need for dietary studies.

Often these traits are described through direct observation, but additional tools such as acoustic telemetry (tracking animal movements through listening devices) can be used to identify natural behaviors in ecosystems. For example Currey *et al*. (2015) used passive telemetry to identify space use of a predatory reef fish showing that moon periods influence size of activity space and foraging identifying a key behavioral trait. This type of behavior would have been difficult to describe without the use of telemetry. In sharks, Meyer *et al*.

(2010) used acoustic telemetry to examined long-term movements of tiger sharks, revealing that some individuals use atolls to forage for juvenile albatross, and others potentially use cognitive maps (recognition of foraging sites used previously) to assist in moving long distances. Tools such as acoustic telemetry can give us a sense of not only where animals are moving, but also describe the behavioural patterns that contribute to their functional roles.

Outside of natural settings, experiments can also help identify the features of organisms that may affect their functional roles. For example, in behavioural experiments, Port Jackson sharks (*Heterodontus porusjacksoni*) have been found to display individual differences in "boldness" and stress management which could influence both habitat selection and prey choice (Byrnes and Brown 2016). Unique behavioral traits are not only seen experimentally. One of the more famous examples of behavioral adaptations of hunting in sharks is from ambush tactics of white sharks (*Carcharodon carcharias*) on juvenile seals in South Africa, which employ breaching behaviors rarely observed in white sharks elsewhere (Martin *et al.* 2005). From these examples, it can be noted that each of these features described assist in determining a species function in their habitat.

Other methods to determine species traits are particularly useful for elasmobranchs. Elasmobranchs are known to vary in fecundity (reproductive success) and age of maturity. Understanding a species' life history traits is vital for trophic study as they can determine specific needs at different stages in growth. For example, cownose rays have been found to exhibit significantly different growth rates and longevity between the Gulf of Mexico and the western Atlantic (Neer and Thompson 2005), meaning possible differences in bioenergetics between the two populations. There can even be differences in life history traits in the same population of a species. For example, a study of the grey reef shark (*C. amblyrhynchos*) population in Palmyra Atoll is one of the first to find variation in life-history without fishing influence (Bradley *et al.* 2017).

Trophic ecology

There are many ways to describe a species ecological role, but the most common approach is to explore its trophic (dietary) interactions within a food web. Trophic interactions are measured through both analysis of stomach contents and biochemical tracers. Stomach contents can directly tell an observer what an organism eats, but there are some limitations. Taxonomic resolution can vary, with some stomach contents requiring genetic barcoding to determine their species identity. Marine organisms without hard/bony structure are digested more quickly, possibly biasing stomach content records towards items that are more difficult to digest. Identifying stomach contents requires a high degree of expertise, which is difficult to achieve without formal training. Stomach contents also tend to indicate recent diet, but may not provide information about long-term dietary preferences. In larger species, depending on angling methods, gastric emptying often occurs before stomach contents can be recovered. Additionally, lethal sampling is often not possible or ethical for species of conservation concern which may significantly reduce sample size. For these reasons, biochemical tracers are increasingly being used alongside stomach content analysis.

Certain macronutrients (i.e. amino acids, carbohydrates, lipids) can be traced through diet and assimilation in tissues. The composition of macronutrients vary due to abiotic and biotic factors and different techniques can be used to determine dietary roles of organisms in their environment. Tracer techniques have common benefits such as being non-lethal, and tending to require fewer samples. The most commonly applied techniques for trophic studies are stable isotope analysis (SIA) (Layman *et al.* 2012), lipid and fatty acid analysis (FA) (Budge *et al.* 2006), and compound specific stable isotopes (CSIA/CSFA) (Budge *et al.* 2008). All of these techniques have their own benefits and limitations which have been thoroughly reviewed (Post 2002; Layman *et al.* 2012; Young *et al.* 2015; Bierwagen *et al.* 2018; Pethybridge *et al.* 2018).

Ecosystem modeling

There are a wide range of ecosystem models that can be used to quantify a species' ecological role. These models provide a mechanism to bring together all the information about functional roles, observation, species biology, environmental processes, and trophic ecology, into a simulated system that allows researchers to test a species role in an ecosystem. Fig. 2 shows the scope and scale of the types of data that can be used in ecosystem models. In general, the more information that can be fed into a model, the better the model will function and the more accurate its predictions will be.

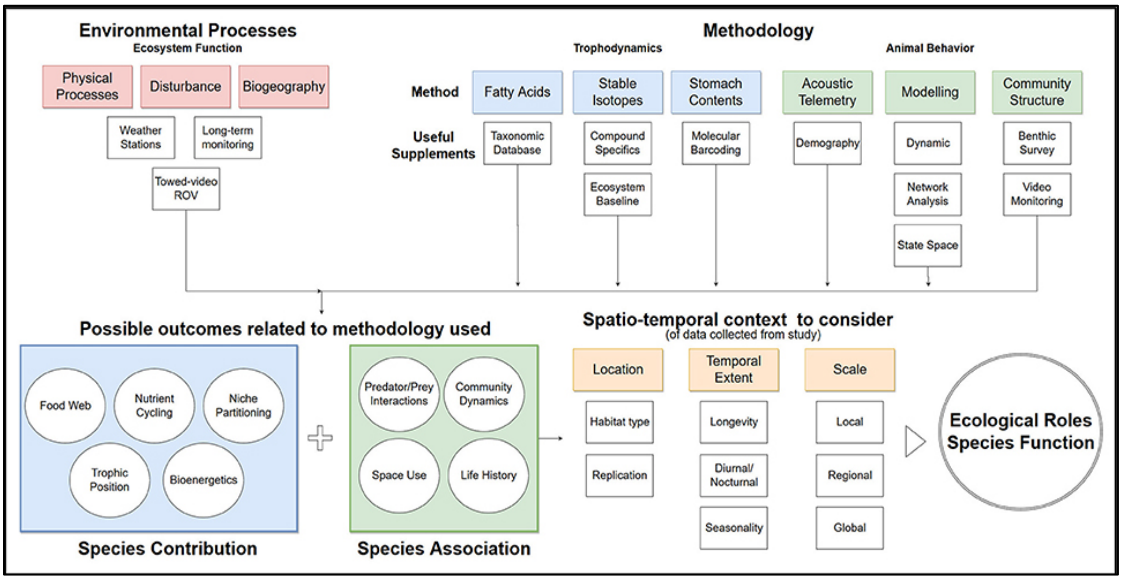


Fig. 2. An overview of the different types of data that can be used to 'populate' an ecosystem model that is used to predict a species' ecological role, and potential consequences of its removal (from Bierwagen *et al* 2018).

Most ecosystem models use inputs that are based on flow of nutrient availability (i.e. Carbon/Nitrogen) or energy (joules). These models also need information related to species traits and function such as habitat use, predator-prey relationships, and food web dynamics. As already mentioned, these traits can vary largely by scale and context, and these variations need to be considered before selecting an ecosystem model (Bierwagen *et al.* 2018; Pethybridge *et al.* 2018). Ecosystem models have been used to determine importance of specific species such as the starry ray (*Raja asterias*) and vulnerability to fishing pressures (Coll *et al.* 2013). However, since many ecosystem models are populated with information from generalized information repositories such as FishBase, many models may be making assumptions that may neglect spatio-temporal variability, especially where data are limited for some species, habitats, and locations.

Concluding remarks on methods

The methods used to understand how sharks and rays function in marine environments are growing increasingly sophisticated and complex, and researchers are using multiple approaches to explore this complex and challenging subject. Using multiple methods, collecting more data, and feeding this information into better models is producing more realistic accounts of shark and ray ecology, and a multiple method approach is certainly preferable to more simplistic approaches.

Nevertheless, researchers are still facing challenges in dealing with environmental complexity, incomplete data, species diversity, and variation across time and location. For example, some sharks are generalists while others are specialists and /or opportunists which can alter their subsequent ecological roles (Munroe 2014). Additionally, changes in historical versus contemporary abundance can also change their ecological roles over time (Coll 2013). Lastly, in complex ecosystem like coral reefs, foodweb complexity dampens predator effects making it more difficult to demonstrate ecological roles (Finke and Denno 2004). Thus, while our understanding of shark and ray ecological roles is increasing, this complexity makes it difficult to upscaling these findings to make generalisations about how sharks and ray function in marine ecosystems, and what the effects of removing them could be.

CURRENT STATE OF KNOWLEDGE: WHAT DO WE KNOW?

The dominant paradigm in shark and ray ecology is that sharks play important ‘top down’ roles in regulating marine ecosystems (e.g. Baum and Worm 2009; Barley *et al.* 2017). This narrative is consistent with ecological theory which has been demonstrated in marine ecosystems, for example, with intertidal systems (Pinnegar *et al.* 2000). Parallels are also sometimes drawn to well known examples in terrestrial ecology. For example, sharks are sometimes compared to top predators such as wolves, with inferences that effects evident in terrestrial ecosystems are likely to be occurring in marine ecosystems (e.g. Wirsing and Ripple 2011; Ripple *et al.* 2014).

Nevertheless, much of our current understanding of the ecological roles of sharks and rays revolves around shark *trophic ecology*, i.e., what different sharks eat and what preys upon them. In many instances, these studies of trophic ecology are used to *infer* the ecological roles of the study species. While these studies provide the theoretical foundation and dietary information to predict shark and ray ecological roles, scientific understanding of shark and ray ecological roles (e.g. how a shark’s trophic ecology affects the ecosystem) is much more limited, largely due to the complexities previously described. As a result, there are relatively few studies that directly examine ecological roles using ecosystem models that incorporate a wide range of data. Furthermore, research has tended to be focused on coral reef ecosystems and scientific understanding of shark trophic ecology in other systems such as deep sea and pelagic ecosystems is relatively poor. There is also much less information on the trophic ecology, and subsequent ecological roles, of batoids (rays, skates and wedgefishes).

Generally, the scientific evidence used to illustrate shark and ray ecological roles revolves around five ‘classic’ research papers that have been cited over 5700 times (Stevens *et al.* 2000; Bascompte *et al.* 2005; Myers *et al.* 2007; Sandin *et al.* 2010; Estes *et al.* 2011). These papers suggest that sharks and rays are top level predators that exert ‘top down’ effects on ecosystems by consuming prey and lower trophic levels. The conventional generalisation is that removing top predators such as sharks will cause trophic imbalances that result in the ‘release’ of prey species when then multiply without predation control, which may result in a ‘trophic cascade’ (see case study Coastal Habitats).

While these papers are compelling, it should be noted that two are theoretical modelling papers, one is a synthesis paper using data from these papers, and the remaining two are highly contentious (see case study Coastal habitats). These papers, and the remaining literature, are also limited by the following factors:

- In general, shark ecological roles are usually discussed in terms of a narrow selection of species, typically larger charismatic top predators, with much less attention focused on the ecological roles of smaller, less charismatic sharks, and less still on rays.

- Evidence for ecological roles are mainly inference based on trophic ecology grounded in ecological theory, and/or based on circumstantial evidence (e.g. comparing fish assemblages and behaviours in high vs low predator density)
- Complexities and controversies are evident across the field (see Coral Reef Habitats, Coastal Habitats, and Pelagic Habitats)

The importance of detail and context

Sharks are commonly considered to be top predators, and sometimes erroneously referred to as apex predators. However, these generalisations can be misleading as spatial and temporal context must be considered when discussion a species' ecological role. For example, the seven gill shark (*Notorynchus cepedianus*) is a large species mainly found in cold and/or deep water. In this environment, it may have few competitors and may well function as an apex predators (Barnett *et al.* 2012). However, the diet and behaviours of seven gill sharks can change from one location to another and between small and larger individuals (Braccini 2008; Abrantes and Barnett 2011), meaning that it's potential ecological role also changes in space and time. Dietary and habitat use changes between juvenile and adult sharks are well document (Grubbs 2010) for many species. These **ontogenetic shifts** mean that as a shark or ray grows, its ecological role will change depending on its diet at the time and where it is living.

As sharks and rays grow in size, they may change their diet and the habitats they use. Thus, their ecological roles also change in space and time.

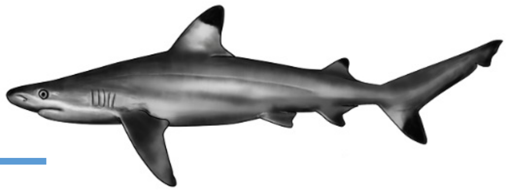
Furthermore, the diversity of sharks means that only adult members of the largest species may be top-level predators, and generalisations that sharks are top level predators need to be made with caution. For example, small species such as the white-spotted bamboo shark (*Chiloscyllium plagiosum*), sharpnose shark (*Rhizoprionodon taylori*) and milk shark (*Rhizoprionodon acutus*) are less than 1 m when fully grown (Fig. 3) and feed mainly on invertebrates (Last and Stevens 2009; Wai *et al.* 2011). These species are common coastal predators, but given their small size and diet, they are clearly not top level predators.

Ecological roles can also change over short periods of time. White sharks and the great hammerhead shark may be considered as apex predators in their respective ecosystem, at least until orcas (*Orcinus orca*) arrive. Orcas are known to hunt and eat large sharks (Pyle *et al.* 1999; Sorisio *et al.* 2006) and thus when present, these apex predators are in fact top predators, not apex predators, and may change their behaviour. It should also be noted that even large coastal apex predators such as the great hammerhead shark (*Sphyrna mokarran*) will be prey for large fishes and even birds during their juvenile phase.

In summary, generalisations that sharks and rays are top level or apex predators should be avoided. The ecological roles of sharks and rays will change as they grow from juveniles to adults (Heupel *et al.* 2014), vary from place to place, and may even change over short periods of time. Furthermore, few sharks are true apex predators. Most sharks and rays could probably be considered as mesopredators (Heupel *et al.* 2014), and the numerous small-bodied sharks and rays that feed on invertebrates could be considered as lower order mesopredators.

Fig. 3. A fully grown milk shark (*Rhizoprionodon acutus*) is less than 1 m in length. While they are a common shark species, their small size and diet indicate that they are not top level predators.
Photo: A.Chin.

HABITAT SPECIFIC ACCOUNTS



Coral reef habitats

Coral reefs are highly diverse and contain nearly 1/4 of all known marine species (Roberts *et al.* 2002; Abrantes and Barnett 2011). Of the approximately 1250 described elasmobranchs to date, around 450 (39%) use tropical marine ecosystems (White and Sommerville 2010). Coral reefs are areas of conservation concern, yet consideration of the ecological role of sharks and rays in these areas is a relatively recent research subject and tends to be fixated on their role in top-down effects on the ecosystem (Osgood and Baum 2015). In the tropical pacific region (East Asia to French Polynesia), 46 species of shark and ray occur on coral reefs (Steene 2003). These species are functionally diverse and range in size and space use. For example, grey reef sharks (*Carcharhinus amblyrhynchos*), whitetip reef sharks (*Triaenodon obesus*), and blacktip reef sharks (*Carcharhinus melanopterus*) are well distributed throughout this region and are more resident to reef habitats. Transient sharks such as bull sharks (*Carcharhinus leucas*) and tiger sharks (*Galeocerdo cuvier*) make large-scale migrations but also use reef areas. Whale sharks (*Rhincodon typus*) also inhabit reef areas and are the largest known shark species, while the epaulette (*Hemiscyllium ocellatum*) is cryptic and small. Ray species can remain small such as the blue spotted mask ray (*Neotrygon kuhlii*) and ribbontail ray (*Taeniura lymma,* ~35cm), but others such as the blotched fantail ray (*Taenuiura meyeini,* ~1.8 m) grow to a large size.

The role elasmobranchs play for coral reef health is an emerging field and a contentious one. Some functional traits are directly quantifiable such as rays modifying habitats through bioturbation (O'Shea *et al.* 2012). Bioturbation behavior in rays benefits smaller organisms by creating shelter and new habitat for settlement of species. Other traits such as trophic function are harder to quantify and information on how dietary roles relate to ecosystem importance is difficult to determine. Recent biochemical (Frisch *et al.* 2016) and network studies (Williams *et al.* 2018) have identified that reef sharks assist in distributing nutrients through nitrogen waste from pelagic sources to reef benthic sources. This nutrient input can be important given that coral reefs are generally nutrient poor, and thus these pelagic inputs subsidise coral reefs and contribute to reef health. A recent bioenergetics model suggest that a resident reef shark community such as grey reef sharks need to eat over 100kg/day (Mourier *et al.* 2016). Thus, in terms of energy flow and nutrient distribution, resident reef sharks could be vital to maintaining reef health. However, other reef-dwellers such as coral trout are also known to feed from pelagic sources (such as planktivorous fish) (Matley *et al.* 2018). For these reasons, it is important to understand how biomass of elasmobranchs compare to other predatory fish.

Shark population size and its effects on coral reef health can vary by biogeographic region. Shark removal has resulted in negative impacts for some remote coral reefs such as atolls in

Western Australia (Ruppert *et al.* 2013), but direct effects of removal are less clear in other areas. Variation in coral reefs can change reef shark abundance, and thus, alter the ecological effect sharks may have on a specific reef. For example, isolated reefs that are biological hotspots with productive upwelling from deep pelagic environments can support large numbers of sharks. For instance, reef sharks / hectare were estimated to be 2-4 on the Great Barrier Reef depending on management zone (Robbins *et al.* 2006), but some authors have claimed densities upwards of 100 sharks per km^2 in the uninhabited atoll areas of the Northern Line Islands (Sandin *et al.* 2008). Fishing and other human impacts can also impact population size. Areas like the Line Islands can be seen as near-pristine, but reefs can also be heavily degraded such as locations like the Caribbean where reef sharks (outside of nurse sharks) were sighted in just over 6% of a 1,000 km^2 area (Ward-Paige *et al.* 2010).

Case study: grey reef sharks (*Carcharhinus amblyrhynchos*): same species, different function

As mentioned above, depending on biogeographic region and bathymetric features, dynamics of shark populations of the same species can change. Without robust estimates of abundance, ecological impacts of the species are impossible to determine. On the Australian GBR, researchers have both determined grey reef sharks to be in decline (Robbins *et al.* 2006; Hisano *et al.* 2011) and stable (Heupel *et al.* 2009). These differences stem from type of population assessment used. On the GBR, grey reef sharks have been shown to suppress behavioral foraging activity of herbivores (Rizzari *et al.* 2014), but also determined to have weak top-down effects (Casey *et al.* 2017). So even in the same region, there is disagreement about how abundant grey reef sharks are, and the impact they have on the ecosystem. In other remote areas such as Moorea in French Polynesia (Mourier *et al.* 2016), and Palmyra atoll such as Hawaii, biomass estimates of grey reef sharks far surpass continental areas with greater human footprint.

Case study: sharks and rays as mesopredators

Resident reef sharks and batoids are considered to be mesopredators (mid-level consumers). The diet of stingrays varies by species, but many reef dwellers occupy soft sediment areas creating feeding pits through fin undulation where they feed on benthic invertebrates (O'Shea *et al.* 2012). They also feed on small fish, cephalopods, and crustaceans (Hollingworth 2005). Diet interpretation for reef sharks is more difficult as they are highly mobile, and the capture of the animals for study often results in gastric emptying. Of the studies available, reef sharks are considered to be generalist feeders feeding from both benthic and pelagic resources. For example, the whitetip reef shark has a diet of mainly teleost fish, but other reef sharks such as the grey reef in addition to teleost fish include eels, cephalopods, and crustaceans (Wetherbee *et al.* 1997; Cortes 1999; Papastamatiou *et al.* 2006). Grey reef sharks previously were thought to be incapable of eating large bodied fish such as grouper based on gape size and trophic levels determined from stable isotopes, re-characterizing their role as apex predator to mesopredator. However, recent discovery of cooperative hunting and direct feeding observation in French Polynesia has shown that in some cases grey reef sharks do take grouper and still occupy an apex predator trophic position (Mourier *et al.* 2016). Hence, for some individuals trophic position of a single species can shift based on both location and life stage.

Scientific debates regarding the ecological roles of sharks and rays on coral reefs

A common emerging theme within study of reef shark diets and roles on coral reefs is that resident reef sharks (grey reef, whitetip, blacktip) are more likely to be mesopredators than larger transient reef associated sharks (e.g. tiger shark, bull shark). The most widely used dietary analysis technique is stable isotope analysis. Niche ratios determined from this type of analysis have found that resident reef sharks overlap in diet with large bodied teleost fish such as coral trout (*Plectropomus leopardus*) and red-throat emperor (*Lethrinus miniatus*) (Frisch *et al.* 2016; Roff *et al.* 2016a; Bond *et al.* 2018). These findings imply that there is functional redundancy between these species, and therefore that reef sharks impose weak top-down effects on these systems. Based on these notions, Roff et al (2016) downgraded the ecological importance of reef sharks on coral reefs. As a response to the assertion of weak top-down effects, Ruppert et al (2016) offered a rebuttal to these statements by claiming that Roff et al (2016) had weak correlative evidence to draw such conclusions. This sparked further debate between these research groups with Roff counter-criticising a study from Ruppert et al (2013) that found evidence of shark-mediated trophic cascades on coral reefs. Roff claimed that the “trophic cascades” found in the Ruppert study were related to community changes following disturbance as opposed to predator mediated effects. The debate ensued with more replies and rebuttals and is still debated today. From this specific case study it should be noted that both of these papers have flaws that need addressing and that there is still little consensus on top-down effect resident reef sharks have on coral reef ecosystems.

Coastal habitats

Coastal habitats are home to a large and diverse array of sharks and rays. The coastal zone is very dynamic and complex, with diverse habitats types including rivers and estuaries, mangroves, coastal sand and mudflats, islands, coral reefs, rocky reefs, kelp beds, seagrass meadows and deeper sandy and muddy habitats. In these systems, productivity is driven by a complex interplay of terrestrial, coastal and oceanic processes. This complexity is reflected in the diversity of sharks and rays in this habitat. Coastal sharks and rays range from large freshwater and estuarine species such as river sharks (*Glyphis spp*) and sawfishes (*Pristis spp*), small sharks such as the milk shark and sharpnose shark, eagle rays (Myliobatidae) and butterfly rays (Gymnuridae), to large sharks and rays such as the tiger shark (*Galeocerdo cuvier*), bull shark (*Carcharhinus leucas*), cownose ray (*Pastinachus sephen*). Together, these species form rich communities of sharks and rays that use coastal habitats as nursery grounds and core habitats (Heupel *et al.* 2007).

Scientific understanding of the ecological roles of coastal sharks mainly focuses on trophic ecology. Unsurprisingly, given the diversity of species and habitats, coastal sharks and rays feed on a wide variety of prey ranging from invertebrates to large marine mammals such as dugongs, feed across many different trophic levels., and may gain their energy from coastal and pelagic sources (Borrell *et al.* 2011). Recent research has even suggested that the bonnethead shark (*Sphyrna tiburo*) may even derive energy from seagrasses which introduces a new dimension to coastal shark trophic ecology (Leigh *et al.* 2018).

Research has also demonstrated that coastal sharks exhibit resource partitioning whereby different species living in the same location use different habitats and/or eat different prey (Navia *et al.* 2007; Abrantes and Barnett 2011; Kinney *et al.* 2011). Large mobile species such as bull sharks may consume a wide variety of prey, and exert predatory pressure over large areas (Daly *et al.* 2013). Variation in trophic ecology is commonplace with species showing ontogenetic shifts in diet and habitat use (Whitty *et al.* 2009; Espinoza *et al.* 2012; Chin *et al.* 2013; Matich and Heithaus 2015), and evidence that what a shark eats can change between locations (Cabrera-Chávez-Costa *et al.* 2010; Abrantes and Barnett 2011). The complexity of habitats and processes and diversity of sharks involved also mean that top down effects of predators may be diffused.

While trophic ecology, ontogeny and niche partitioning are well understood, there are very few studies on the ecological role of coastal sharks and rays. One study on Greenland sharks (*Somniosus microcephalus*) suggest that this species is an apex predator that may play a regulatory role in Arctic ecosystems (McMeans *et al.* 2013). Nevertheless, this example is from a simple ecosystem where the Greenland shark is the only shark species inhabiting those waters, and no other predators are present that could fill that role (McMeans *et al.* 2013). Additionally, this role is again inferred from dietary information. Nevertheless, perhaps the most well known case study of a **trophic cascade** involves the effects of coastal shark declines in the United States.

Case study: evidence and controversy regarding trophic cascades in coastal sharks

One of the most highly cited papers in shark ecology is that by Myers *et al*. (2007). This paper, published in the prestigious journal *Science*, proposed that a reduction on the abundance of coastal sharks such as sandbar sharks (*Carcharhinus plumbeus*), bull sharks, tiger sharks, and hammerhead sharks, reduced predation pressure on mesopredators such as the cownose ray (*Rhinoptera bonasus*) such that cownose ray populations rapidly increased. These rays then consumed so many scallops that they caused the collapse of the scallop fishery.

This purported trophic cascade was very compelling in presenting a correlation between multiple population trends and is perhaps the best known example of a shark mediated trophic cascade. Unfortunately, this study has been largely discredited. A series of scientific rebuttals, culminating with comprehensive rebuttal by Grubbs *et al*. (2016), noted several critical flaws in the study.

1. The rapid increase in cownose rays is biologically impossible given that this species only produces one pup every two years.
2. The study ignored other data sets showing that coastal shark populations were increasing at the same time (Fig 4).
3. Dietary studies showed that scallops are only a minor part of the cownose ray's diet.

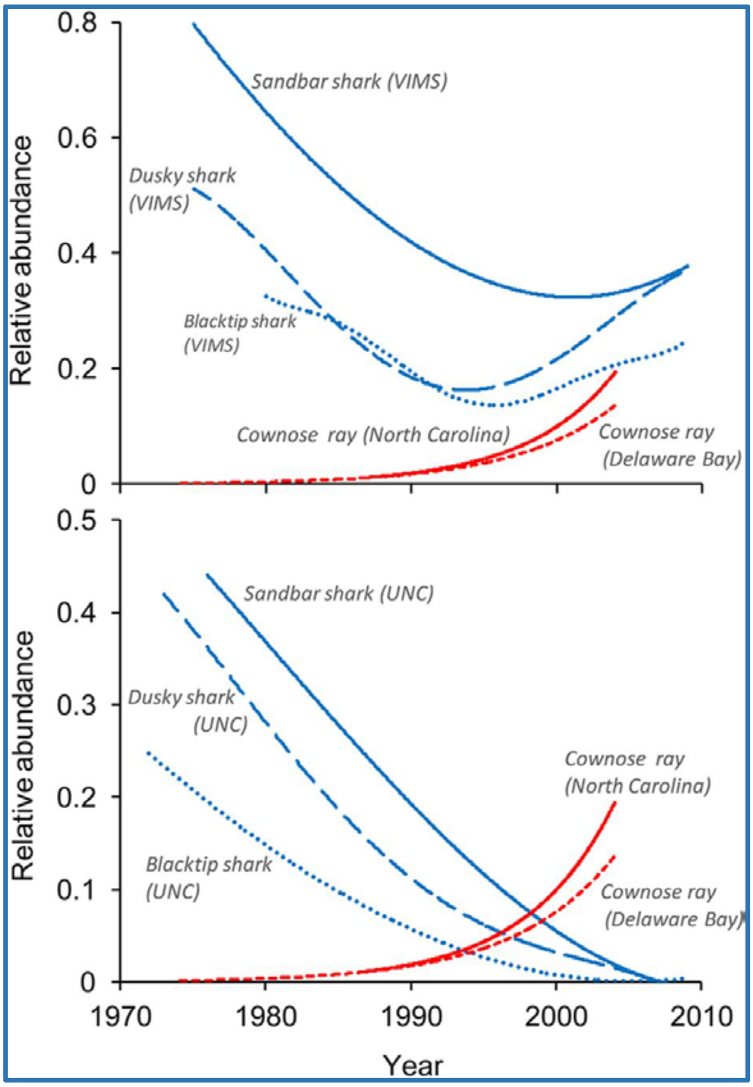


Fig. 4. More complete data showing that coastal shark populations were increasing at the time the cownose rays increased which calls into question the veracity of the trophic cascade reported by Myers *et al*. 2007. Figure from Grubbs *et al*. 2016, used under Creative Commons licence 4.0.

Meanwhile, there is good evidence that coastal sharks such as tiger sharks, and large bodies stingrays can have wider ecological effects. However, these effects are not through direct predation affecting prey abundance, but rather through modifying the behavior of other species or by creating micro habitats. These effects are discussed in detail in the section 'Beyond Predation'.

Deep ocean habitats

Deep ocean habitats are considered here as habitats extending from the edge of the continental slope (nominally 200 m depth) to the abyssopelagic zone thousands of meters deep. The deeper depths of the bathypelagic zone (1000 – 4000 m depth) are extreme environments characterised by cold water temperatures, darkness, and pressure. Habitats are general soft silt and sediment with rocky features or 'outcrops'. Biological productivity is reduced as nutrient and energy cycling must occur without photosynthesis. These extreme environments mean that relatively few species of sharks and rays live in these habitats. Most deep water sharks live in shallower depths of the mesopelagic zone (to 1000m depth). Deep water sharks may also make vertical migrations which blurs the distinction between pelagic and deep water species.

Deep water sharks and rays include the gulper sharks (Centrophoridae), cowsharks (Hexanchidae), dogfishes (Squalidae), lantern sharks (Etmopteridae), kitefin sharks (Dalatiidae), and sleeper sharks (Somniosidae), and many of the skates (Rajidae). As for other sharks and rays, there is a great diversity of size, body shape and life history patterns. The pygmy lantern shark (*Etmopterus fusus*) may be the smallest of the sharks, growing to 29 cm (Last and Stevens 2009), while a bluntnose sixgill shark (*Hexanchus griseus*) is 17 times larger, reaching 4.8 m in length. This diversity in size suggests that deep water sharks may play a wide range of ecological roles. Of note are the cookie cutter sharks (*Isistius spp*). Even though these species only grow to half a meter in length, they could arguably be considered as apex predators as they feed on large fishes and cetaceans.

Little is known about the ecology and behaviour of deep water sharks due to the inaccessibility of these species. Scientific understanding mainly revolves around trophic ecology, with the diets of different species studied from specimens captured in deep water fisheries (e.g. Kousteni *et al.* 2017) or from chemical analyses (e.g. Pethybridge *et al.* 2011). Deep water sharks mainly prey upon fishes and cephalopods (cuttlefishes, squids, and octopus), although some species also eat crustaceans and may scavenge off 'food falls' (Ebert *et al.* 1992) (see Case study). Deep water sharks can be grouped into three main trophic guilds: benthic predators, bentho-pelagic predators, and pelagic predators (Valls *et al.* 2017). Skates have also been found to eat a wide range of prey including decapods, polychaetes, and fishes, and occupy similar trophic levels as sharks (Ebert and Bizzarro 2009).

As with other sharks and rays, the dietary patterns vary widely, and thus so too would potential ecological roles. There is considerable evidence of niche separation and ontogenetic shifts in deep water species (Braccini 2008; Pethybridge *et al.* 2011; Albo-

Puigserver *et al.* 2015; Valls *et al.* 2017). For example, the diet of the longnose spurdog (*Squalus blainville*) changes with size, and even between the sexes. Fatty acid and diet analysis showed that different deep water sharks in the same region feed on different prey; chimaeras acting as low-order and benthic consumers; medium-sized dogfish preying upon squids and fishes; catsharks as predators of cephalopods, and larger and deeper dwelling dogfish as predators on bathypelagic fish and squids, and also potentially scavenging off marine mammal carcasses (Pethybridge *et al.* 2011). Dietary partitioning may minimize inter-specific competition for resources. A further complication is that a single species' dietary patterns, and thus potential ecological roles, can differ between locations (Morato *et al.* 2003; Abrantes and Barnett 2011). These variations imply that ecological roles will be highly variable and context specific.

The ecological roles of deep water sharks and rays are generally inferred from their diet. For example, due to their large size and diet, cowsharks (Hexanchidae), which include the six and seven gill sharks, are thought to be apex predators as there are no other species known to fulfil a similar predatory role in those habitats (Barnett *et al.* 2012). This suggestion aligns with ecological theory of predator-prey dynamics. However, these relationships are *inferred* from dietary data and ecological theory, and there is no direct evidence that deep sea sharks and rays have widespread ecological effects. Nevertheless, it is known that they can act as vectors for energy and nutrient flow.

Case study: sharks and rays as vectors for nutrient and energy transfer

Sharks and rays can act as important vessels that transport energy and nutrients between deep and shallow waters. The Chillean devil ray (*Mobula tarapacana*) has been found to dive to depths of up to almost 2000 m to feed on dense deep water prey such as fishes and squids before returning to the surface (Thorrold *et al.* 2014). This behaviour effectively collects energy and nutrients from the deep sea and transports them to the surface layers of pelagic habitats which can be very nutrient poor.

Sharks and rays may also transport nutrients and energy from surface levels to the deep sea. When large sharks and ryas such as whale sharks and mobulids die, they sink to the sea floor and thus transport energy from the surface to deeper waters (Higgs *et al.* 2014). These food falls can support mobile deep water scavengers (Fig. 5). Interestingly, the authors of thus study suggest that these types of food fall may be more common than previously thought, with all four food falls in this study found in with a 1.5 km^2 area. It may be that such food falls are responsible for a significant amount of carbon that reaches the deep sea, and that a relatively high proportion of surface production may reach deep sea habitats in this manner (Higgs *et al.* 2014).

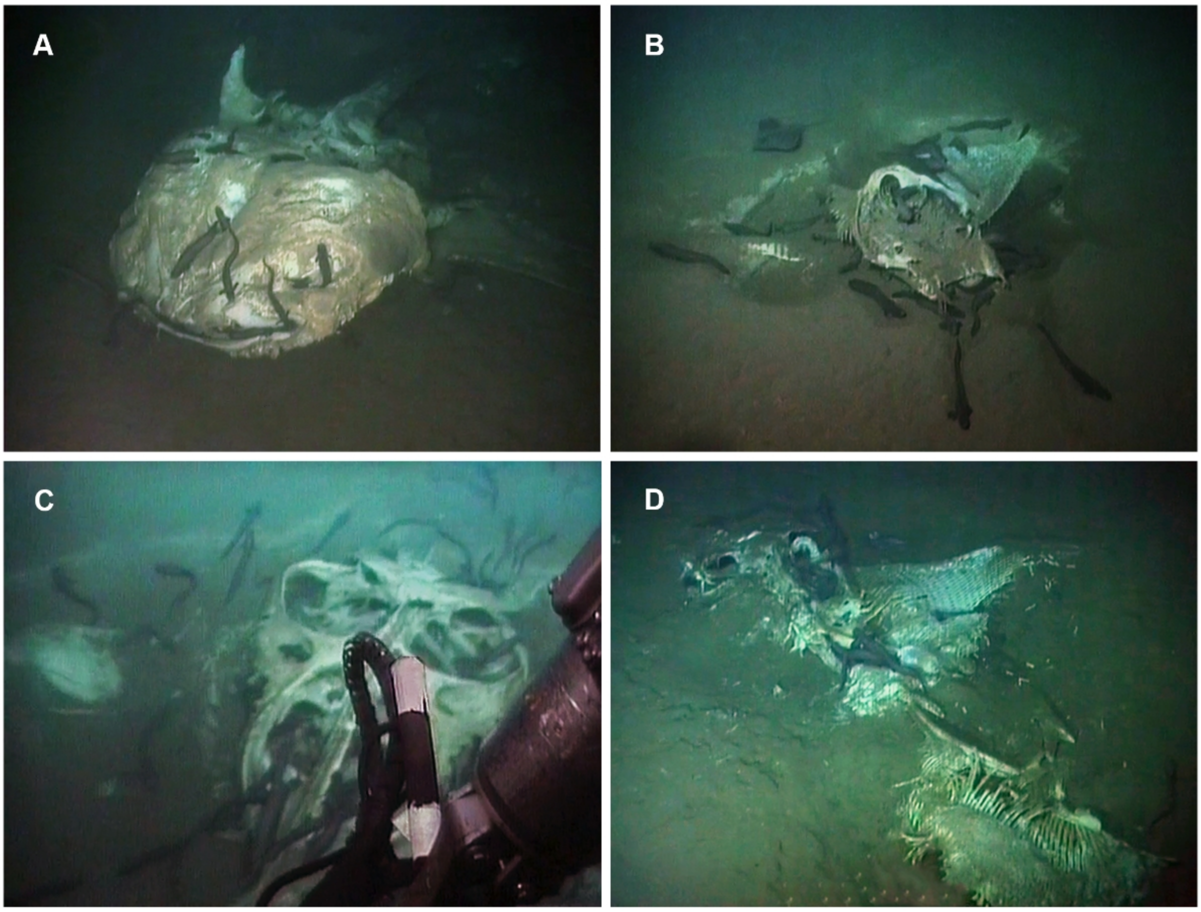


Fig. 5. Upon their death, large sharks and rays like this whale shark (A) and mobulids (B-D) transfer energy and carbon from surface levels to deep sea habitats where they can be taken up by mobile scavengers. Figure reproduce from Higgs *et al*. 2014 under Creative Commons Attribution License.

Pelagic habitats

Pelagic environments have relatively low shark and ray diversity (~31 species) compared to other habitats and occupy mainly epipelagic (~0-200 m) and mesopelagic (~200-1000 m) zones. This comprises about 6% of the total number of Chondrichthyes (Camhi *et al.* 2009). Common examples include cookie cutter shark (*Isistius spp*), pelagic stingray (*Pteroplatytrygon violacea*), mako shark (*Isurus oxyrinchus*), hammerhead (*Sphyrna spp*), thresher sharks (*Alopias spp*), white shark (*Carcharodon carcharias*), silky shark (*Carcharhinus falciformis*), blue shark (*Prionace glauca*), oceanic whitetip (*Carcharhinus longimanus*), whale shark (*Rhincodon typus*), manta ray (*mobula spp*).

The term “pelagic” encompasses species that are mobile and do not associate with seafloors. Within the pelagic group, “oceanic” elasmobranchs spend part of their time in coastal or shelf areas. Large marine mammals and fishery-targeted schooling fishes also occupy these areas. The conservation status of these species are difficult to determine as many are a target of the shark fin trade and pelagic shark catches are often under- reported.

However, many of these species appear to be in decline and vulnerable to over-exploitation (Dulvy *et al.* 2008). While there is conservation concern for pelagic elasmobranchs, ecological studies are limited and often data deficient.

Pelagic systems have long been thought to be driven by bottom-up processes because of nutrient fluxes in the biogeochemical cycling, but top-down control has been suggested for some specific areas (Horswill *et al.* 2016). Pelagic environments have a large supply of prey resources including large blooms of krill and zooplankton. The main dietary component of pelagic predators comes from micro-nekton (2-20cm) consisting of crustaceans, cephalopods, and small fishes (of these including schooling species such as clupeids) (Young *et al.* 2015).

Case study: the need to know the numbers

> "These catch rate analyses generated almost immediate contrary responses by several fishery scientists….It is therefore critical that blue shark standardized CPUE series are evaluated in terms of their reliability as a potential index of abundance."
>
> -Aires-da-Silva et al

Without an idea of abundance and population density, it is difficult to determine the type of influence sharks may have on the ecosystem, particularly in the trophic space as biomass and energy transfer is an important component. However, in pelagic habitats the lack of data on populations creates debate. The authors Baum (2003) and Baum and Myers (2004) found rapid, severe declines (>75% in the past 15 years) in species such as the hammerhead, mako, and thresher shark abundances in the Northwest Atlantic and Gulf of Mexico. Two studies, Burgess (2005) and Aires-da-Silva (2007) found that CPUE estimates of decline were less than reported and the Baum studies did not consider factors such as current stock assessments. Baum replied with criticism of those studies, ignored their claims and in 2009 linked their previous studies to cascading top-down effects in a pelagic ecosystem suggesting predator-mediated trophic cascades. Given that there were multiple authors that offered alternatives to these findings, Baum made broad conclusions of ecological roles with limited evidence. (Baum *et al.* 2003; Baum and Myers 2004; Baum *et al.* 2005; Burgess *et al.* 2005; Aires-da-Silva *et al.* 2008)

Case study: not all pelagic sharks share diet

While it is understood that micro-nekton are an important dietary component of shark species, there are few studies that offer comparative and comprehensive analysis of diet between pelagic species. Off South Australia, a study of 417 shark stomachs collected from fisheries totaling five species (bronze whaler, shortfin mako, dusky, smooth hammerhead, and common thresher sharks) (Rogers *et al.* 2012). While all species were found to feed of a suite of cephalopods, crustaceans and teleost fish, distinctions in dietary niche were found between some species. The authors found evidence of diet specialization in both the common thresher and the shortfin mako which are highly migratory. The authors also found shelf-association in species such as dusky and bronze whalers. This study brings insights into diet preferences of these animals, where high degrees of specialisation may impact food webs in ways that are not yet understood.

BEYOND PREDATION

The ecological roles of sharks and rays are most commonly viewed through the effects of predation, that is, sharks or rays consuming prey and thus altering their abundance which leads to additional effects through the foodweb. However, predators such as sharks and rays can also have ecological effects through their presence and behaviours.

The ecology of fear

There is compelling evidence that predators can influence ecosystems even without consuming prey through the 'ecology of fear' (Wirsing *et al.* 2008; Heithaus *et al.* 2012). In Western Australia, observational data, tracking studies and experiments have shown that the presence of tiger sharks, which are apex predators in the shallow seagrass systems of Shark Bay, can lead to more abundant seagrass growth. Tiger sharks are key predators on marine turtles and dugongs. When tiger sharks are present, turtles and dugong appear to be more vigilant and alter their seagrass foraging behavior, reducing the intensity of their feeding. This in turn, leads to increased seagrass length and density, and changes in seagrass community composition (Burkholder *et al.* 2013). These behavioral effects have been termed *behaviour-mediated trophic cascades* (Burkholder *et al.* 2013) and it is possible that may other such relationships exist but have yet to be discovered.

On a smaller scale, the presence of grey reef sharks and large predatory fishes has also been shown to alter prey behavior, changing the way herbivorous fishes such rabbit fishes (*Siganus spp*) and unicorn fishes (*Naso spp*) graze on algae (Rizzari *et al.* 2014). These species are important grazers in coral reefs that help maintain balance between coral and algae.

Other observations require further investigations. For example, it is widely reported that stingrays, wedgefishes and guitar fishes sometimes form large multi-species groups (rafts) in shallow waters. This behavior is believed to be an anti-predator defensive behavior (Semeniuk and Dill 2006). These species are large bodied and relatively common in coastal and coral reef habitats that likely play important roles in these systems (see below). However, the localized effects of this rafting behavior are unknown, as are the potential ecosystem effects should predators be removed and these species begin foraging with impunity.

> The presence of predators such as sharks may change the behavior of prey species, causing 'behaviour-mediated trophic cascades' in seagrass systems, or affecting the grazing behavior of herbivorous fishes on coral reefs.

Habitat engineers and facilitated feeding

While the ecological roles of batoids (rays, wedgfishes, skates, and guitafishes) are poorly studied, there is emerging evidence that some species play unusual roles in coastal and coral reef habitats as 'habitat engineers' and through facilitated feeding.

When large rays such as cownose rays or whiptail rays (*Himantura spp*) feed, they excavate a pit by 'blowing' water into the substrate and through fin movements. This behavior turns over the sediment so that the rays can find the buried invertebrates that comprise a large part of their diet. However, this behavior has wider effects for other species.

The mixing and turn-over of sediments by species is termed *bioturbation* and it is an important ecological process that can affect the chemical and microbial composition of sediments, including oxygen content (Mermillod-Blondin and Rosenberg 2006). Research on stingrays in Western Australia has found that these species could turn over 42% of the surface sediments in a coastal bay over a year, and likely play a significant role in the sediment ecology in that area (O'Shea *et al.* 2012).

Another effect of this behaviour is facilitated feeding. As the rays are excavating their pits, they stir up a lot of sediment and expose many other invertebrates that escape. These invertebrates may be important food sources for other species and foraging rays are often accompanied by an escort of other fishes that feed on the newly exposed prey (Fig. 5) (VanBlaricom 1982). This effect has been called facilitated feeding or facilitated provisioning, as the rays are enabling other species to feed. Importantly, this effect extends beyond small reef fishes to larger predatory fishes such as jacks (*Carangidae*) (Kiszka *et al.* 2014), cobia (Smith and Merriner 1982), and even higher up the food web to birds such as cormorants (Kajiura *et al.* 2009).

Lastly, once the animal moves onto to begin digging another pit, the existing pit may persist for several days, forming microhabitats for other species. Indeed, some invertebrates have been found to preferentially colonise these pits, suggesting that the presence of ray feeding pits may affect the distribution and density of invertebrate populations (VanBlaricom 1982).

Fig. 5. The feeding activities of stingrays such as this cowtail ray (*Pastinachus sephen*) creates micro habitats for invertebrates, turns over sediment, and exposes prey which facilitates foraging for other species.

Photo: A. Chin

CURRENT UNDERSTANDING OF SHARK AND RAY ECOLOGICAL ROLES

The habitats accounts and case studies illustrate the complexity and diversity of shark and ray ecology, and also highlight the limitations in scientific understanding. It is evident that most of what is known revolves around trophic ecology, and that in most cases, ecological roles are inferred by collecting information about diet and predation, and extrapolating it to predict ecosystem effects using principles of ecological theory. While inference is warranted in many examples, clear ‘cause and effect’ data are still lacking. Other studies have used comparisons between fished (few sharks) and pristine (many sharks) reefs to infer how sharks may alter the ecosystem. However, these studies are compromised by spatial variation, missing baseline data, and the trends are correlative, not causative. Furthermore, these patterns are inconsistent between reefs in different areas and the role of reef sharks remains contested. Overall, few studies provide compelling data that demonstrate the ecological roles of sharks and rays.

Nevertheless, while clear evidence of the ecological role of sharks and rays is limited, dietary studies, emerging evidence of behavioural effects, and ecological theory support inferences that sharks and rays may play important roles in maintaining ecosystems. Indeed, the diversity of sharks and rays, complexity of marine environments, and the magnitude of data needed to demonstrate such links may mean that it may not be possible to unequivocally demonstrate their ecological roles. Thus, in spite of the limited data, their potential to play important ecological roles should not be dismissed due to lack of supporting evidence.

To reconcile these contradictions and manage the complexity of the issue, we propose a series of summative statements and illustrative case studies about shark and ray ecological roles, with each statement being qualitatively assessed to describe the risk associated with each statement.

Descriptive criteria

This diversity of species and information quantity and quality poses challenges for managers and conservation practitioners in understanding and communicating messages about the ecological roles of sharks and rays. There are operational and reputational risks in supporting a claim that may be contested or based on limited information. In order to consistently and explicitly describe the scientific veracity of claims about the purported ecological roles of sharks and rays in the marine environment, a series of Descriptive Criteria have been assigned to each claim based on the available scientific evidence and case studies described above. These Criteria describe the claim’s (1) Likelihood of being true; (2) amount of supporting evidence; and (3) the amount of consensus and agreement between studies (and scientists) about each claim. These criteria enable managers and conservation practitioners to thus gauge the potential risks in applying these claims.

	Low	Medium	High
Likelihood of being accurate	**Implausible**: Does not align with ecological theory AND/OR contradicts known species' biology, ecology, and behavior. L	**Plausible**: Some aspects align with ecological theory AND with understanding of species' biology, ecology, and behavior. L	**Highly plausible**: Congruent with ecological theory and understanding of species' biology, ecology, and behavior. L
Level of supporting evidence	**Limited evidence**: Evidence limited to a single study on a single species and location. E	**Moderate evidence**: Two to three studies on several species and in multiple locations. E	**Strong evidence**: Four or more studies involving multiple studies and locations. E
Scientific consensus & agreement	**Contested**: widespread scientific disagreement and inconsistent opinions about the veracity of the claim. C	**Some agreement**: general agreement about the claim, although differing opinions about how widely it can be applied. C	**Strong agreement**: scientific consensus about the claim albeit with a small number of known exceptions. C

CASE STUDIES, SUMMATIVE STATEMENTS AND GENERAL FINDINGS

In spite of the complexity of interactions between species, environmental factors, and variation across space and time, several case studies, or 'stories' have emerged that demonstrate the ecological roles sharks and rays can play in marine ecosystems. These can be used as illustrative case studies to create statements about the ecological roles of sharks and rays, however, they are context specific.

Summary findings are also presented regarding the ecological roles of sharks and rays in each of the habitats explored. In general, strong definitive statements for these habitats cannot be made (with the exception of the statements below). Nevertheless, these summaries provide a concise summary of the findings for each habitat type.

Lastly, this section concludes with general findings that apply across all species and habitat types. These findings should be carefully considered when developing summative statements about the ecological roles of sharks and rays, as they provide valuable context and caveats that affect the potential risk of misinterpretation and misuse of such statements.

Illustrative case studies

From the information collected, several clear case studies or 'stories' have emerged that clearly show the potential ecological effects of sharks and rays in marine ecosystems. These case studies have strong scientific evidence, but are very case specific. Nevertheless, it is possible that these same relationships exist elsewhere, but have not yet been documented. Each of the following statements have been ranked using the descriptive criteria of Likelihood; Evidence; and Consensus to provide an indication of the potential risk in promoting that statement.

L = Likelihood
E = Evidence
C = Consensus

Tiger sharks play important ecological roles in seagrass ecosystems in Western Australia

🟢 L 🟡 E 🟢 C

Tiger sharks can act as apex predators in shallow coastal seagrass systems. The very presence of these predators can alter the foraging behavior of large herbivores such as marine turtles and dugongs. Fear of predation keeps these herbivores moving which reduces grazing pressure on seagrass meadows, resulting in denser and more abundant seagrass growth in these areas (Wirsing *et al.* 2008; Heithaus *et al.* 2012; Burkholder *et al.* 2013).

Grey reef sharks can affect the grazing behavior of herbivorous fishes

🟢 L 🔴 E 🟢 C

The presence of sharks (and other mesopredators) can affect the grazing behavior of fishes, resulting in reduced grazing rates and range at localised scales (Rizzari *et al.* 2014). However, the implications of these effects at reef-wide scales are unclear.

Benthic rays can create microhabitats and facilitate feeding for other species

L E C

Large benthic stingrays such as the cowtail ray (*Pastinachus sephen*) can create feeding pits in soft sediment that may persist over tidal cycles. Their foraging behavior stirs up sediment, turning over nutrients, and forming micro-habitats for other species (O'Shea *et al.* 2012). Stingray foraging can also assist foraging by fishes (Smith and Merriner 1982; Kiszka *et al.* 2014) and even birds (Kajiura *et al.* 2009).

Sharks and rays can play important roles in transferring energy and nutrients between marine ecosystems

L E C

As mobile marine species sharks and rays can play important roles in collecting, storing, and moving energy from one part of the ocean to another. Reef sharks such as the grey reef shark have been found to move energy and nutrients from pelagic ecosystems to coral reefs, thus supplementing nutrient limited coral reef ecosystems (Williams *et al.* 2018). Large rays and whale sharks can also move energy and nutrients between the shallow photic levels and deep - ocean zones by vertical migrations and food falls (Higgs *et al.* 2014; Thorrold *et al.* 2014).

Summative statements by habitat

L = Likelihood
E = Evidence
C = Consensus

Coral reef habitats

Coral reef habitats contain a relatively well known assemblage of sharks and rays. They are very complex and diverse habitats which complicate efforts to clearly demonstrate the ecological role of reef sharks and rays. Some relationships are evident, but research findings are often contradictory and claims are highly contested.

- Coral reef sharks and rays are likely to act as meso-predators on most reefs. L E C
- Functional reduncancy between sharks shouldn’t be assumed L E C

Reef sharks can cause reefs to have higher fish abundance and diversity, but these patterns are very case specific, evidence is contradictory and consensus is low.	🟡 L	🟡 E	🔴 C
Reef sharks can transport energy from pelagic food webs to coral reefs.	🟢 L	🟡 E	🟡 C
The presence of reef sharks can alter the behaviour and subsequent grazing of herbivorous fishes	🟢 L	🔴 E	🟢 C

Coastal habitats

Coastal habitats include a wide range of habitats and a very diverse group of sharks and rays. Most information about these species is about their trophic ecology with ecological effects inferred, however data are generally limited.

Coastal sharks and rays are very diverse and exhibit a wide range of trophic relationships, niche partitioning, and ontogenetic shifts in diet and habitat use.	🟢 L	🟢 E	🟢 C
There is little evidence that coastal sharks and rays play significant ecological roles through predation in coastal ecosystems.	🟡 L	🔴 E	🟢 C
Large sharks such as tiger sharks may play a significant ecological role in coastal ecosystems through behaviour-mediated trophic cascades, however examples are very case specific.	🟢 L	🟡 E	🟢 C

Deep water habitats

Deep water habitats are extreme habitats characterized by low light levels, cold temperatures and increased pressure. Nevertheless, a wide range of sharks and rays occupy these depths, but mostly above 1000 m. Fishes and cephalopods are very important dietary components for these species. Deep water habitats have unique drivers and processes that drive biological productivity.

Large deep water sharks may act as apex predators and play important ecological roles in these systems. However, this is inferred, and variation in diet suggests that ecological roles may also vary, even within the same species.	🟢 L	🟡 E	🟡 C
Sharks and rays may be important vectors for transferring energy and nutrients between deep and shallow ocean zones.	🟢 L	🟡 E	🟢 C

Pelagic habitats

The pelagic environment is relatively featureless and nutrient poor, making it a challenging environment. Biological productivity is variable in space and time, and driven by both bottom up (e.g. upwellings and plankton blooms) and top down (predation). Species diversity is relatively low, and pelagic sharks and rays are highly mobile, including vertical migrations to the deep sea habitats. Fishes and cephalopods are the main prey, although pelagic sharks may opportunistically feed on seabirds and marine mammals. Most information is about trophic ecology, with ecological roles inferred, although some ecological modeling studies have been completed.

- There is limited evidence that pelagic sharks and rays play significant ecological roles in pelagic environments. However information is very limited and trends are highly contested.

L **E** **C**

General findings

Apart from the habitat specific findings and illustrative case studies, the literature review process and the information collated form the review have highlighted several general concepts and findings that apply across all species and habitats.

In general:

- The ecological effects of sharks and rays will be more diffuse and/or harder to detect in more complex ecosystems (i.e. more species, habitats, and processes occurring).
- Generalisations about the ecological roles of sharks and rays cannot be made. There are too many species and too much variation. Additionally, different populations of the same species can have different diets in different locations.
- The diversity of shark and ray sizes, diets, and ecology suggests that as a group, they may affect marine ecosystems at multiple levels in multiple ways (including being prey for other species). While these effects may be diffuse, managers should not be complacent about the potential effects of removing large numbers and/or functional groups of these species.
- Few sharks are true apex predators, and these are restricted to adults of large species such as seven gill sharks, white sharks, and great hammerhead sharks. However, even these species may be displaced from the apex predator role in the presence of other supra-predators such as orcas.
- Most sharks and rays are mesopredators or top level predators.
- Many sharks and rays change their trophic ecology over their lifespans, and thus, their ecological roles will also change in space and time.
- There is little evidence that sharks and rays are keystone species.

- There are no scientific reports or case studies that specifically demonstrate that sharks keep prey populations healthy by eating genetically inferior individuals. While this seems plausible and is consistent with the theory of natural selection, there are no scientific data that demonstrate this relationship.
- It is important to remember that demonstrating ecological effects is extremely challenging. It is possible that sharks do play critical ecological functions, and some may even be keystone species, but there is currently insufficient data to demonstrate these effects.
- This lack of data increases uncertainty. It is possible that declines of a shark or ray could result in unforeseen ecological consequences. The potential for such 'shock and surprises' should be factored into conservation planning, and the precautionary principle may be a useful principle to consider.
- It is important to recognise that much of the research on shark and ray trophic ecology occurs in altered ecosystems. Changing environmental conditions and human impacts are likely to affect the nature and detectability of ecological relationships such as trophic cascades.
- Managers also need to consider that the ecological effects of removing sharks and rays may be exacerbated where fishing pressure or other impacts have reduces ecosystem resilience, for example by depleting other species that could fulfil similar functional roles to sharks and rays.

OPTIONS FOR COMMUNICATIONS

Providing specific recommendations about communications and conservation messaging is beyond the scope of this review. However, the following guidance may be of value in developing and framing conservation messages regarding the ecological importance of sharks and rays, and the need for their conservation in maintaining healthy marine ecosystems.

- Statements about the ecological roles of sharks and rays must always be placed into **specific context**, i.e., discuss a specific species in a specific location that is supported by cite able scientific evidence, and use the correct terminology.
- **Case studies** of specific species and interactions can be a good tool to communicate these concepts to the general public. These are digestible 'stories' of species and places that the public can connect to.
- Conservation messaging may need to be presented more holisticly. There does seem to have been an over focus on ecological roles.
- Conservation messages could be **framed as a package** that highlights the importance of conserving the biological, ecological, social, cultural, and economic values of sharks and rays.

- This holistic messaging approach may also **reduce the risk** of relying on just one conservation rationale, which in the case of ecological roles, may be based on incomplete data.
- There is also the potential to frame sharks as **indicator species**, as sharks and rays are likely to be noticeably depleted through excessive fishing pressure.

FUTURE DIRECTIONS

Further research on the ecological roles of sharks and rays is urgently needed to better understand the ecological risks of depleting shark and ray populations, and thus inform management and conservation efforts. While advances in research and understanding are being made, many knowledge gaps remain including basic dietary information for many species. Nevertheless, the field is rapidly evolving with new technology and emerging techniques, and some long standing paradigms are being revisited. There is no doubt that this is a challenging field of research, which may partially explain the current lack of knowledge. Nevertheless, new techniques and technology will allow new research questions to be explored and improve scientific understanding of the ecological roles of these species.

The following research areas and activities should be carefully considered to improve current knowledge.

- Basic dietary and trophic ecology data are still needed for many species. For example, the diet and bioenergetics of the grey reef shark, a widespread commonly encountered species, still needs to be comprehensively documented.
- Molecular barcoding of prey species, and even of empty stomach linings, should be considered in dietary studies to provide more precise data on shark and ray diets.
- Studies of trophic ecology should use multiple methods to ensure a complete account of a species diet.
- More research needs to be done on predation behavior and trophic relationships at night, i.e. nocturnal research. Acoustic telemetry and new cameras could help overcome historical constraints on this type of research.

Lastly we would urge researcher working in this field to be open minded and receptive of the complexity and variability of ecological roles and trophic relationships. These interactions are highly likely to change across space and time, and rejecting contradictory data offhand is not serving the broader scientific interest. We encourage researchers to be more collaborative and communicative, and to make genuine efforts to resolve differences of opinion in a collegiate manner. Some of the big questions left to be answered are probably best tackled through multi-disciplinary teams using complimentary approaches.

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