

ORIGINAL ARTICLE



WILEY

Buried in the sand: Uncovering the ecological roles and importance of rays

Kathryn I. Flowers  | Michael R. Heithaus  | Yannis P. Papastamatiou 

Institute of Environment, Department of Biological Sciences, Florida International University, North Miami, FL, USA

Correspondence

Kathryn I. Flowers, Institute of Environment, Department of Biological Sciences, Florida International University, 3000 NE 151st Street, North Miami, FL 33181, USA.
Email: katie.flowers.90@gmail.com

Funding information

Mays Family Foundation

Abstract

Rays (superorder Batoidea) are the most diverse group of elasmobranchs, and many are threatened with extinction. However, there remain areas where research on the ecology of this group is lacking, from trophic interactions to their importance to ecosystem structure and function. Such ecological insights are critical for predicting the potential consequences of changes in their population sizes. Our aim was to synthesize the existing ray ecology literature and identify key knowledge gaps in order to provide a framework for future research. Numerous studies describe ray diets, and the number of studies using biochemical methods to address ray trophic interactions is increasing. The implications of ray predator–prey interactions on population dynamics of prey and how ray foraging might influence ecosystem dynamics through bioturbation remain relatively unexplored, despite claims that rays are ecologically important because they are bioturbators and because of their potential to deplete stocks of commercially important bivalves. Therefore, to better integrate rays in our understanding of marine community dynamics, there is a need to: (i) combine behavioural data with dietary information to describe predator–prey interactions; (ii) understand how ray bioturbation affects biogeochemical cycles and infaunal communities; (iii) elucidate conditions under which rays might initiate or transmit trophic cascades through consumptive and non-consumptive pathways; and (iv) consider anthropogenic influences on the ecological roles and importance of rays.

KEYWORDS

Batoidea, bioturbation, fishing, predator–prey interactions, symbiosis, trophic ecology

| | | | | | |
|-----|--|-----|-----|---|-----|
| 1 | INTRODUCTION | 106 | 3 | CURRENT UNDERSTANDING OF RAY EFFECTS ON ECOSYSTEMS | 112 |
| 2 | PREDATOR–PREY INTERACTIONS | 106 | 3.1 | Potential impacts on prey densities | 112 |
| 2.1 | Who is eating whom? | 106 | 3.2 | Effects of direct predation and risk on wider community | 113 |
| 2.2 | Using diet information to understand sympatric species coexistence | 111 | 3.3 | Bioturbation and nutrient dynamics | 114 |
| 2.3 | Anti-predator behaviour by rays | 112 | | | |

| | | |
|-----|--|-----|
| 3.4 | Facilitation and other symbiotic relationships | 116 |
| 4 | ANTHROPOGENIC DRIVERS OF RAY ECOLOGY | 116 |
| 4.1 | Predicting ray responses to climate change | 116 |
| 4.2 | Fisheries impacts | 117 |
| 4.3 | Interactions with tourism | 117 |
| 5 | CONCLUSION AND PATH FORWARD | 118 |
| | ACKNOWLEDGEMENTS | 119 |
| | DATA AVAILABILITY STATEMENT | 119 |
| | REFERENCES | 119 |
| | SUPPORTING INFORMATION | 119 |

1 | INTRODUCTION

Rays (superorder Batoidea: skates, stingrays, electric rays and shovelnose rays) are widely distributed in freshwater, brackish, shallow coastal and deep-sea environments (Aschliman et al., 2012; Last et al., 2016). Despite being widespread and, in some cases, commercially important, this group of fishes has received less scientific attention than most vertebrate groups (Aschliman et al., 2012; Bräutigam et al., 2015). Rays evolved in the Lower Jurassic period (Aschliman et al., 2012), and among vertebrates, their proportional risk of extinction is high and exceeded only by that of amphibians (Last et al., 2016). Rays are threatened primarily by overfishing, with benthic species being particularly susceptible to trawl and gill-net fisheries and semi-pelagic species being vulnerable to longline and drift net fisheries (Dulvy et al., 2014). Rays are also valuable to tourism industries around the world, with ray watching tourism generating millions of dollars in multiple countries (Haas, Fedler, & Brooks, 2017; O'Malley, Lee-Brooks, & Medd, 2013; Vaudo et al., 2018). Knowledge of the ecological role and importance of rays is needed in order to understand how species declines or, in some cases predatory or competitive release, may affect ecosystem function and structure. Such an understanding can be important for making appropriate management decisions for species and ecosystems. It is likely that we will underestimate the importance of some rays like large sawfishes (Pristidae) and skates (Rajidae) given widespread declines that preceded modern ecological reporting (Stevens, Bonfil, Dulvy, & Walker, 2000). Local ecological knowledge about trophic interactions involving rays offers valuable insight into more pristine ecosystems (e.g. Bonfil et al., 2018). It is plausible that under pre-disturbed conditions, large sawfishes and skates acted as top predators.

A key distinction when evaluating the ecology of any species is the difference between ecological roles and importance. The ecological role of an organism mainly considers its trophic position, but can include any type of interaction, regardless of its significance to the functioning of whole ecosystems, while the ecological importance of a species considers the consequences of a change in species

abundance to community structure and function (Heithaus, Frid, Vaudo, Worm, & Wirsing, 2010). The ecological roles and importance of rays were reviewed briefly by Heithaus et al. (2010), and a recent review by Martins, Heupel, Chin, and Simpfendorfer (2018) highlighted several ecological roles of rays in relation to nursery areas. Here, we expand on these previous reviews to consider ray ecological roles and importance across taxa and all life stages, and identify gaps in our current understanding to develop a prospectus for future research. We assessed peer-reviewed primary literature published as of 04 October 2018 using a variety of search term combinations (Table S1) in Google Scholar (<https://scholar.google.ca>). Several key papers published after our original search have been included in this review due to their importance to the field of study. Relevant citations found in original research articles were also included, leading to an examination of > 500 studies. It was not possible to describe every study in this review; therefore, we have focused on central examples from the literature that was assembled. Only two of the 26 described ray families were not represented in the literature from our search (Hexatrygonidae and Pleisiobatidae). Taxonomic classifications reported are based on Last et al. (2016), with the exception of devil rays (Mobulidae) that are based on Hosegood et al. (2018). Figure 1 outlines ray interactions with other species and the environment that will be explored in this paper.

2 | PREDATOR-PREY INTERACTIONS

2.1 | Who is eating whom?

Approximately 60% of the ray ecology literature (320 of 520 publications) examines basic trophic relationships, and multiple species have had their diets extensively studied. For example, stomach contents of the thornback skate (*Raja clavata*, Rajidae) have been described in 18 studies throughout its range in the Eastern Atlantic Ocean and Mediterranean Sea (e.g. Ajayi, 1982). The diets of 198 ray species were documented in the literature (Table S2), with only four of the 26 ray families not represented (Hexatrygonidae, Narkidae, Pleisiobatidae, and Zanobatidae). Although rays primarily consume crustaceans, molluscs, teleosts and worms (Table S2), diets varied within and among species, across life stages, spatially and temporally. Sex differences in diets occur in some species (e.g. Delpiani, Spath, & Figueroa, 2013; Lipej, Mavrič, Paliska, & Capapé, 2013; Orlov, 1998), which may be due to sexual dimorphism, spatiotemporal segregation and increased energetic requirements during gestation (Delpiani et al., 2013). Many rays showed seasonal and/or regional variation in diet, which has been hypothesized to be related to changes in prey availability, abundance and distribution (Barbini & Lucifora, 2011; Bornatowski, Robert, & Costa, 2010; Braccini & Perez, 2005; Kadri, Saïdi, Marouani, Bradai, & Bouaïn, 2013; Molina & Cazorla, 2015; Saglam, Ak, Kutlu, & Aydin, 2010; Saglam & Bascinar, 2008; San Martin, Braccini, Tamini, Chiaramonte, & Perez, 2007; Szczepanski & Bengtson, 2014), but could also be related to ray seasonal migrations influenced by environmental variables (Schlaff, Heupel, &

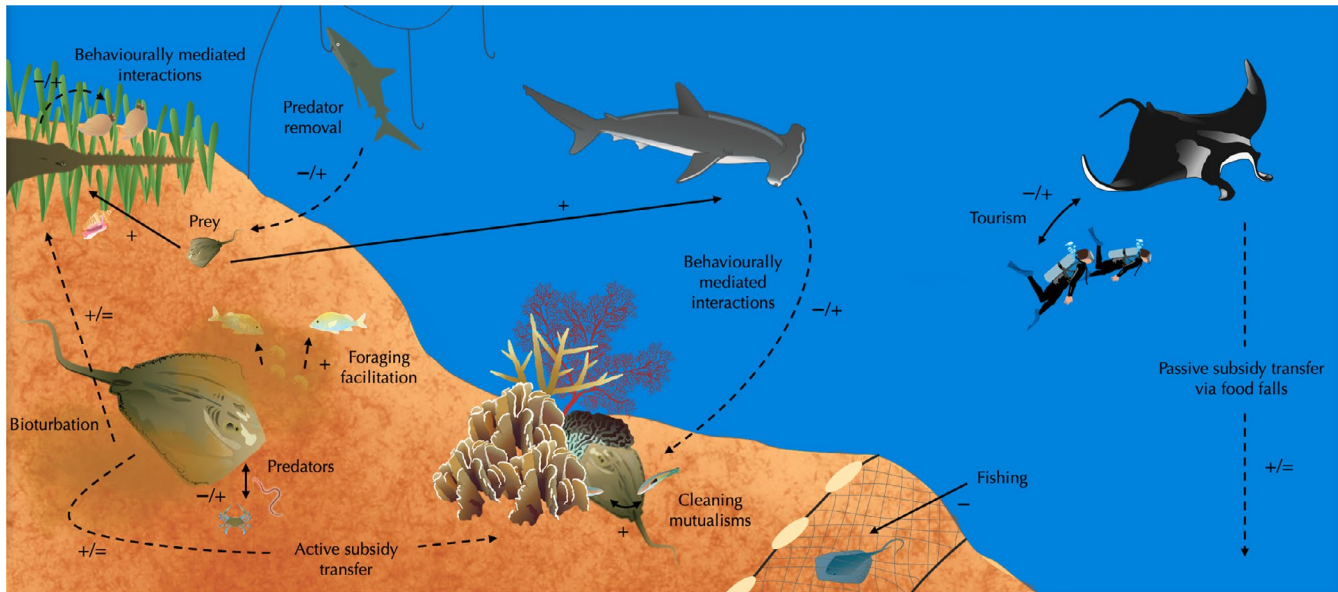


FIGURE 1 Conceptual diagram of the interactions between rays, other species and their environment in a coral reef system. Solid black arrows represent direct effects, while dashed arrows represent indirect effects. “+” represents a positive effect, “-” a negative effect and “=” no effect or an insignificant effect relative to other processes. Rays directly provide energy to other species as a prey source and indirectly via foraging facilitation. Cleaning mutualisms are assumed to provide positive benefits for the ray and cleaner fishes. In some cases, rays negatively affect prey densities via direct predation. However, in other cases ray foraging can benefit prey through refugia created after pit formation or by promoting diversity and smoothing out distribution patterns. While rays turn over high volumes of sediment, the effect of bioturbation may be negligible compared to other biogeochemical processes like tidal flux and ocean currents. Nutrients released during this process may be transferred across habitats, which could affect ecosystem productivity. Nutrients may also cross habitat boundaries by ray behaviour (e.g. feeding in seagrass habitat and defecating on reefs) and as food falls post-mortem. Vigilance by filter-feeding bivalves in response to the presence of ray predators may reduce their propensity to feed; however, in some cases it is possible that behaviourally mediated effects could promote coexistence. Similarly, top-down effects on rays by predators like sharks may negatively affect ray densities or push them into unprofitable habitats. However, behaviourally mediated effects may also stabilize ray populations. The loss of top predators may lead to positive benefits for the ray population (ray release) or negative consequences resulting from density-mediated effects following increases in population size. Fishing generally has a negative effect on ray populations, unless sustainably managed. Tourism can provide conservation benefits for rays but may also lead to a decrease in overall body condition if not properly managed. Images courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/), with the exclusion of the Caribbean reef shark, which was created using Pixelmator v. 3.8.5

Simpfendorfer, 2014). Ontogenetic shifts in ray diets are widespread, where larger prey items were consumed with increasing body size (e.g. Brown, Bizzarro, Cailliet, & Ebert, 2012). While some rays are consuming prey items based on availability (e.g. Ajemian, Powers, & Murdoch, 2012), others may be specializing on particular prey taxa. For example, in an Argentinian scallop fishery where yellownose skates (*Zearaja chilensis*, Rajidae) were collected for a diet study, by-catch is primarily made up of invertebrates, yet the most common prey items in yellownose skate stomach contents were teleosts (Lucifora, Valero, Bremec, & Lasta, 2000). Understanding changes in diet and prey selection is useful for determining the ability of rays to impact prey populations across space and time.

Ray trophic levels (TL) reported in the literature ranged from 3.1 to 4.5, suggesting that most rays are secondary to tertiary level consumers (Table 1). These TLs are comparable to the standardized values calculated for skates (3.48–4.22; Ebert & Bizzarro, 2007) as well as for stingrays and electric rays (3.10–4.24; Jacobsen & Bennett, 2013). TLs varied by species, location and in some cases by individual, while the comparison of different methodologies (i.e. stable isotope analysis versus stomach content analysis) showed slight

variation in the TL value (Burgess et al., 2016; Yemişken, Forero, Megalofonou, Eryilmaz, & Navarro, 2018). Trophic level increased with body size for some species like the longtail stingray (*Hypanus longus*, Dasyatidae; Navia, Mejía-Falla, López-García, Giraldo, & Cruz-Escalona, 2016), the polkadot skate (*Dipturus chinensis*, Rajidae; Hara, Furumitsu, & Yamaguchi, 2018), the rasptail skate (*Rostoraja velezi*, Rajidae; Navia et al., 2016), the southern banded guitarfish (*Zapteryx xyster*, Trygonnorhinidae; Navia et al., 2016) and the yellow-spotted fanray (*Platyrrhina tangi*, Platyrrhinidae; Yamaguchi, Furumitsu, Tanaka, & Kume, 2012); however, body size is not always indicative of trophic position (Barría, Coll, & Navarro, 2015). Small rays such as the Persian Gulf torpedo ray (*Torpedo sinuspersici*, Torpedinidae; mean weight 1.4 kg [Rastgoo, Navarro, & Valinassab, 2018]) and the longtail butterfly ray (*Gymnura poecilura*, Gymnuridae; mean weight 3.8 kg [Rastgoo et al., 2018]) had high TLs (4.5; Rastgoo & Navarro, 2016; Rastgoo et al., 2018), while larger species such as the shark ray (*Rhina ancylostoma*, Rhinidae; mean weight 77.4 kg [D’Alberto, White, Chin, & Simpfendorfer, 2019]) and the spotted eagle ray (*Aetobatus ocellatus*, Aetobatidae; mean weight 41.4 kg [D’Alberto et al., 2019]) had relatively low TLs (3.2; Borrell,

TABLE 1 Ray trophic levels (TLs) reported in the literature, rounded to the nearest decimal. Mean TL was calculated when studies only reported TLs across (1) seasons, (2) size classes or (3) cardinal directions (north, east, south, west). Stomach content analysis (SCA) was the most common methodology used to assess TLs; therefore, TLs calculated from stable isotope analysis (SIA) were only reported when TLs from SCA were not available

| Species | Trophic level (TL) | Method | Section References |
|---|--------------------|--------|--|
| Speckle skate (<i>Raja polystigma</i> , Rajidae) | 3.1 | SCA | Barría et al. (2015) |
| Spotted eagle ray (<i>Aetobatus ocellatus</i> , Aetobatidae) | 3.2 | SIA | Vaudo and Heithaus (2011) |
| Bullnose eagle ray (<i>Myliobatis freminvillei</i> , <i>Myliobatidae</i>) | 3.2 | SCA | Szczepanski and Bengtson (2014) |
| | 3.5 | SCA | Woodland, Secor, and Wedge (2011) |
| Southern eagle ray (<i>Myliobatis goodei</i> , Myliobatidae) | 3.2 | SCA | Molina and Cazorla (2015) |
| Cowtail ray (<i>Pastinachus sephen</i> , Dasyatidae) | 3.2 | SCA | Rastgoo et al. (2018) |
| | 3.3 | SCA | Rastgoo and Navarro (2016) |
| Shark ray (<i>Rhina ancylostoma</i> , Rhinidae) | 3.2 | SIA | Borrell et al. (2011) |
| Giant manta ray (<i>Mobula birostris</i> , Mobulidae) | 3.4 | SIA | Burgess et al. (2016) |
| Giant devil ray (<i>Mobula mobular</i> , Mobulidae) | 3.4 | SIA | Sampson, Galván-Magaña, De Silva-Dávila, Aguíñiga-García, and O'Sullivan (2010) |
| American cownose ray (<i>Rhinoptera bonasus</i> , <i>Rhinoptera</i>) | 3.4 | SCA | Bornatowski, Wosnick, et al. (2014) |
| Freshwater whiplay (<i>Urogymnus dalyensis</i> , Dasyatidae) | 3.4 | SIA | Every et al. (2017) |
| Boreal skate (<i>Amblyraja hyperborea</i> , Rajidae) | 3.5 | SIA | McKinney et al. (2012) |
| Brown stingray (<i>Bathytoshia lata</i> , Dasyatidae) | 3.5 | SCA | Dale, Wallsgrave, Popp, and Holland (2011) |
| Scaly whiplay (<i>Brevitrygon walga</i> , Dasyatidae) | 3.5 | SCA | Rastgoo et al. (2018) |
| | 3.6 | SCA | Rastgoo and Navarro (2016) |
| Sharpnose skate (<i>Dipturus oxyrinchus</i> , Rajidae) | 3.5 | SCA | Barría et al. (2015) |
| | 3.6 | SCA | Mulas et al. (2015) |
| Giant guitarfish (<i>Glaucostegus typus</i> , Glaucostegidae) | 3.5 | SIA | Vaudo and Heithaus (2011) |
| <i>Himantura</i> sp. (Dasyatidae) | 3.5 | SIA | Vaudo and Heithaus (2011) |
| Southern stingray (<i>Hypanus americanus</i> , Dasyatidae) | 3.5 | SCA | Tilley, López-Angarita, and Turner (2013a) |
| Blackspotted whiplay (<i>Maculabatis astra</i> , Dasyatidae) | 3.5 | SIA | Vaudo and Heithaus (2011) |
| Bentfin devil ray (<i>Mobula thurstoni</i> , Mobulidae) | 3.5 | SIA | Sampson et al. (2010) |
| Broad cowtail ray (<i>Pastinachus ater</i> , Dasyatidae) | 3.5 | SIA | Vaudo and Heithaus (2011) |
| Pink whiplay (<i>Pateobatis fai</i> , Dasyatidae) | 3.5 | SIA | Vaudo and Heithaus (2011) |
| Zipper sand skate (<i>Psammobatis extenta</i> , <i>Arhynchobatidae</i>) | 3.5 | SCA | Braccini and Perez (2005) |
| Whitesnout guitarfish (<i>Pseudobatos leucorhynchus</i> , <i>Rhinobatidae</i>) | 3.5 | SCA | Navia et al. (2016) |
| Spotted skate (<i>Raja montagui</i> , Rajidae) | 3.5 | SCA | Barría et al. (2015) |
| Chilean round ray (<i>Urotrygon chilensis</i> , Urotrygonidae) | 3.5 | SCA | Oñate-González, Amezcua, Buszkiewicz, Castellanos-Cendales, and Amezcua-Linares (2017) |
| | 3.6 | SCA | Silva-Garay et al. (2018) |
| Roger's round ray (<i>Urotrygon rogersi</i> , Urotrygonidae) | 3.5 | SCA | Navia et al. (2016) |
| Shortnose guitarfish (<i>Zapteryx brevirostris</i> , <i>Trygonorrhinidae</i>) | 3.5 | SCA | Bornatowski, Wosnick, et al. (2014) |
| Bering skate (<i>Bathyraja interrupta</i> , Arhynchobatidae) | 3.6 | SCA | Kemper, Bizzarro, and Ebert (2017) |
| Longnose skate (<i>Beringraja rhina</i> , Rajidae) | 3.6 | SCA | Kemper et al. (2017) |
| Sharpnose guitarfish (<i>Glaucostegus granulatus</i> , <i>Glaucostegidae</i>) | 3.6 | SIA | Borrell et al. (2011) |
| Large-eye stingray (<i>Hypanus marianae</i> , Dasyatidae) | 3.6 | SCA | Costa, Thayer, and Mendes (2015) |
| <i>Mobula</i> sp. (Mobulidae) | 3.6 | SIA | Borrell et al. (2011) |

(Continues)

TABLE 1 (Continued)

| Species | Trophic level (TL) | Method | Section References |
|--|--------------------|--------|---|
| Speckled guitarfish (<i>Pseudobatos glaucostigmus</i> , Rhinobatidae) | 3.6 | SCA | de la Rosa-Meza, Sosa-Nishizaki, and de la Dueva-Salcedo (2013) |
| Chola guitarfish (<i>Pseudobatos percellens</i> , Rhinobatidae) | 3.6 | SCA | Bornatowski, Wosnick, et al. (2014) |
| Shovelnose guitarfish (<i>Pseudobatos productus</i> , Rhinobatidae) | 3.6 | SCA | Valenzuela-Quiñonez, Galván-Magaña, Ebert, and Aragón-Noriega (2018) |
| Spotted guitarfish (<i>Rhinobatos punctifer</i> , Rhinobatidae) | 3.6 | SCA | Rastgoo and Navarro (2016); Rastgoo et al. (2018) |
| Whitespotted wedgefish (<i>Rhynchobatus djiddensis</i> , Rhinidae) | 3.6 | SCA | Razzaghi, Mashjoor, and Kamrani (2017) |
| | 4 | SCA | Abdurahiman, Nayak, Zacharia, and Mohamed (2010) |
| Smallnose fanskate (<i>Sympterygia bonapartii</i> , Arhynchobatidae) | 3.6 | SCA | Estalles, Perier, and Di Giacomo (2016) |
| <i>Aetomylaeus</i> sp. (Myliobatidae) | 3.7 | SIA | Borrell et al. (2011) |
| Whitespotted skate (<i>Dentiraja cerva</i> , Rajidae) | 3.7 | SCA | Treloar et al. (2007) |
| Whitespotted whiplay (<i>Maculabatis gerrardi</i> , Dasyatidae) | 3.7 | SCA | Rastgoo and Navarro (2016); Rastgoo et al. (2018) |
| Arabian banded whiplay (<i>Maculabatis randalli</i> , Dasyatidae) | 3.7 | SCA | Rastgoo et al. (2018) |
| Leopard numbfish (<i>Narcine leoparda</i> , Narcinidae) | 3.7 | SCA | Navia et al. (2016) |
| Yellow-spotted fanray (<i>Platyrrhina tangi</i> , Platyrrhinidae) | 3.7 | SCA | Yamaguchi et al. (2012) |
| Shortfin sand skate (<i>Psammobatis normani</i> , Arhynchobatidae) | 3.7 | SCA | Mabragaña and Giberto (2007) |
| Pacific guitarfish (<i>Pseudobatos planiceps</i> , Rhinobatidae) | 3.7 | SCA | Silva-Garay et al. (2018) |
| Thornback skate (<i>Raja clavata</i> , Rajidae) | 3.7 | SCA | Morato, Solà, Grós, & Menezes (2003) |
| | 3.9 | SCA | Yemişken et al. (2018) |
| | 4.1 | SCA | Barría et al. (2015) |
| Rio skate (<i>Rioraja agassizi</i> , Arhynchobatidae) | 3.7 | SCA | Bornatowski, Wosnick, et al. (2014) |
| <i>Rhynchobatus</i> sp. (Rhinidae) | 3.7 | SIA | Borrell et al. (2011) |
| | 3.8 | SIA | Vaudo and Heithaus (2011) |
| Spinytail round ray (<i>Urotrygon aspidura</i> , Urotrygonidae) | 3.7 | SCA | Navia et al. (2016) |
| Australian thornback skate (<i>Dentiraja lemprieri</i> , Rajidae) | 3.8 | SCA | Treloar et al. (2007) |
| Polkadot skate (<i>Dipturus chinensis</i> , Rajidae) | 3.8 | SCA | Hara et al. (2018) |
| Diamond stingray (<i>Hypanus dipterurus</i> , Dasyatidae) | 3.8 | SCA | Silva-Garay et al. (2018) |
| Longtail stingray (<i>Hypanus longus</i> , Dasyatidae) | 3.8 | SCA | Navia et al. (2016) |
| | 3.9 | SCA | López-García, Navia, Mejía-Falla, and Rubio (2012) |
| Chilean eagle ray (<i>Myliobatis chilensis</i> , Myliobatidae) | 3.8 | SCA | Silva-Garay et al. (2018) |
| Bleeker's whiplay (<i>Pateobatis bleekeri</i> , Dasyatidae) | 3.8 | SIA | Borrell et al. (2011) |
| Atlantic starry skate (<i>Raja asterias</i> , Rajidae) | 3.8 | SCA | Barría et al. (2015) |
| | 3.9 | SCA | Coll, Navarro, and Palomera (2013); Navarro, Coll, Preminger, and Palomera (2013); Yemişken et al. (2018) |
| Brown skate (<i>Raja miraletus</i> , Rajidae) | 3.9 | SCA | Kadri, Marouani, Bradai, and Bouaïn (2014) |
| Rough skate (<i>Raja radula</i> , Rajidae) | 3.9 | SCA | Kadri et al. (2013) |
| Rasptail skate (<i>Rostroraja velezi</i> , Rajidae) | 3.9 | SCA | Navia et al. (2016) |
| Bignose fanskate (<i>Sympterygia acuta</i> , Arhynchobatidae) | 3.9 | SCA | Barbini and Lucifora (2016) |

(Continues)

TABLE 1 (Continued)

| Species | Trophic level (TL) | Method | Section References |
|---|--------------------|--------|---|
| Southern banded guitarfish (<i>Zapteryx xyster</i> , Trygonorrhinidae) | 3.9 | SCA | Navia et al. (2016) |
| Cuckoo skate (<i>Leucoraja naevus</i> , Rajidae) | 4 | SCA | Barriá et al. (2015) |
| Peruvian eagle ray (<i>Myliobatis peruvianus</i> , Myliobatidae) | 4 | SCA | Silva-Garay et al. (2018) |
| Green sawfish (<i>Pristis zijsron</i> , Pristidae) | 4 | SCA | Razzaghi et al. (2017) |
| Smallthorn sand skate (<i>Psammobatis rudis</i> , Arhynchobatidae) | 4 | SCA | Mabragaña and Giberto (2007) |
| Bight skate (<i>Dipturus gudgeri</i> , Rajidae) | 4.1 | SCA | Treloar et al. (2007) |
| Spiny butterfly ray (<i>Gymnura altavela</i> , Gymnuridae) | 4.1 | SCA | Barriá et al. (2015) |
| | 4.2 | SCA | Yemişken et al. (2018) |
| Pelagic stingray (<i>Pteroplatytrygon violacea</i> , Dasyatidae) | 4.1 | SCA | Varghese, Somvanshi, and Dalvi (2014) |
| Clearnose skate (<i>Rostroraja eglanteria</i> , Rajidae) | 4.1 | SCA | Woodland et al. (2011) |
| Banded guitarfish (<i>Zapteryx exasperata</i> , Trygonorrhinidae) | 4.1 | SCA | Blanco-Parra, Galván-Magaña, Márquez-Farías, and Niño-Torres (2012) |
| Broadnose skate (<i>Bathyraja brachyurops</i> , Arhynchobatidae) | 4.2 | SCA | Belleggia et al. (2008) |
| Largetooth sawfish (<i>Pristis pristis</i> , Pristidae) | 4.2 | SCA | Thorburn, Gill, and Morgan (2014) |
| | 4.5 | SIA | Every et al. (2017) |
| Melbourne skate (<i>Spiniraja whitleyi</i> , Rajidae) | 4.2 | SCA | Treloar et al. (2007) |
| Great torpedo (<i>Tetronarce nobiliana</i> , Torpedinidae) | 4.2 | SCA | Barriá et al. (2015) |
| Marbled torpedo (<i>Torpedo marmorata</i> , Torpedinidae) | 4.2 | SCA | Barriá et al. (2015) |
| Ocellate torpedo (<i>Torpedo torpedo</i> , Torpedinidae) | 4.2 | SCA | Barriá et al. (2015) |
| <i>Pristis</i> sp. (Pristidae) | 4.3 | SIA | Borrell et al. (2011) |
| Longtail butterfly ray (<i>Gymnura poecilura</i> , Gymnuridae) | 4.5 | SCA | Rastgoo and Navarro (2016); Rastgoo et al. (2018) |
| Persian Gulf torpedo (<i>Torpedo sinuspersici</i> , Torpedinidae) | 4.5 | SCA | Rastgoo and Navarro (2016); Rastgoo et al. (2018) |
| Yellownose skae (<i>Zearaja chilensis</i> , Rajidae) | 4.5 | SCA | Belleggia et al. (2016) |

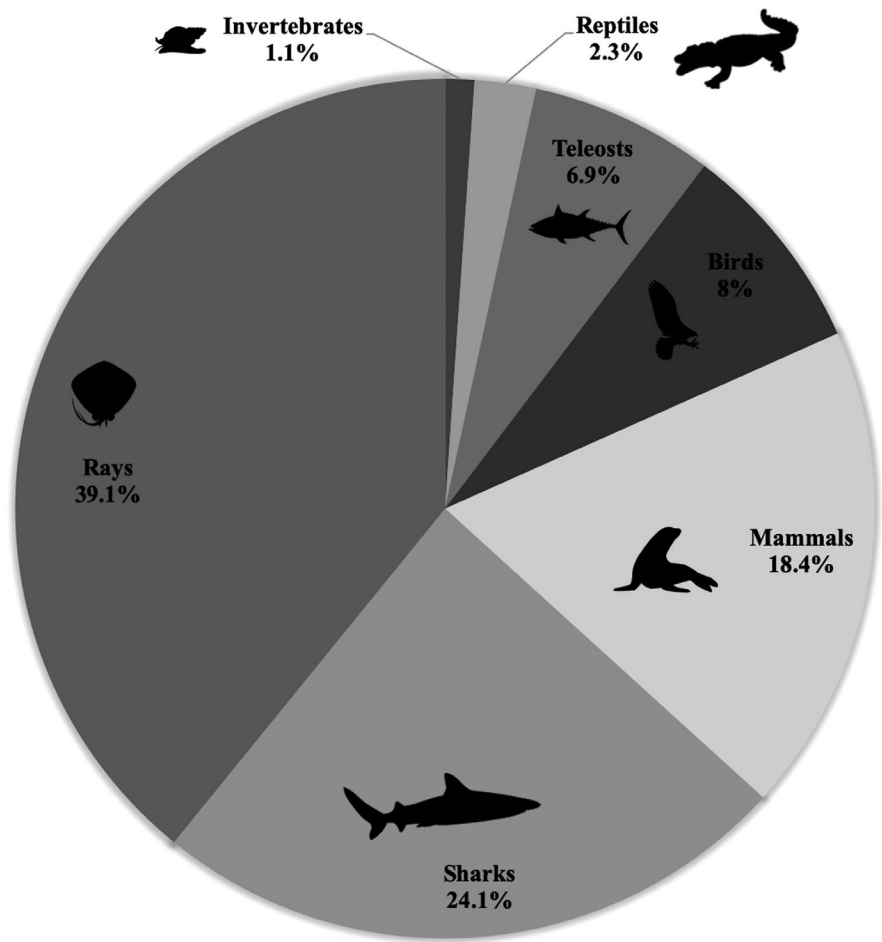
Cardona, Kumarran, & Aguilar, 2011; Vaudo & Heithaus, 2011). Due to the differences in diet with maturity and size, future work should report juvenile and adult diets and TLs separately (Navia et al., 2016). Where possible, we have reported TLs by life stage (Table S3).

A diverse array of organisms feed on rays including other elasmobranchs, teleosts, mammals, birds, invertebrates and reptiles (Table S4). Rays were found most commonly in the diet of elasmobranchs and mammals (Figure 2). Rays (Dasyatidae and Rhinobatidae) are important prey items for great hammerhead sharks (*Sphyrna mokarran*, Sphyrinidae; Cliff, 1995), and thorny skates (*Amblyraja radiata*; Rajidae) are important prey for Greenland sharks (*Somniosus microcephalus*, Somniosidae) in western Greenland (index of relative importance = 84.38; Yano, Stevens, & Compagno, 2007). In New Zealand, killer whales (*Orcinus orca*, Delphinidae) use unique benthic hunting strategies to capture rays (Visser, 1999). A killer whale was observed catching 15 rays (Dasyatidae and Myliobatidae) in one day, which may suggest these whales are ray specialists (Visser, 1999). Coyotes (*Canis latrans*, Canidae) have been found with ray spines and vertebrae (Dasyatidae and Rhinobatidae) in their scat, likely a result of scavenging on carcasses that wash ashore (Rose &

Polis, 1998). Rays consume other rays (within and across families) and this behaviour is most common among skates (Table S4). Certain skate species like the yellownose skate consume conspecifics (Koen Alonso et al., 2001) and members within the same family (e.g. Barbini & Lucifora, 2011). Similarly, adult female southern stingrays (*Hypanus americanus*, Dasyatidae) have been found with large-eye stingrays (*Hypanus marianae*, Dasyatidae) in their stomachs (Branco-Nunes, Albuquerque, Nunes, Oliveira, & Hazin, 2016). Stingray (Dasyatidae) spines have been found in wedgefish, guitarfish and sawfish jaws (Dean, Bizzarro, Clark, Underwood, & Johanson, 2017), while stingray DNA was identified in faecal samples of the smalltooth sawfish (*Pristis pectinata*, Pristidae) along with a stingray tail in the mouth of a captured individual (Poulakis et al., 2017). Rays feeding on other rays is likely opportunistic.

Diet information can provide valuable insight into predator-prey dynamics. Since many ray species have had their diets comprehensively studied and the majority of rays feed on the same major taxa, research should focus on placing this information in broader context with behavioural data. For example, predicting the consequences of shifts in community dynamics will require

FIGURE 2 Proportional representation of ray predator taxa based on the total number of predator species described in the literature ($N = 88$). Graphics downloaded from www.phylopic.org made available by CC0 1.0 Public Domain Dedication and Public Domain Mark 1.0 licences (whelk excluded). Whelk drawn using Pixelmator v. 3.8.5



combining short term diet descriptions (i.e. from stomach content analyses) with longer term diet descriptions (i.e. from stable isotope analyses) and working to understand these descriptions in relation to predator and prey behaviour (Heupel, Knip, Simpfendorfer, & Dulvy, 2014). Specifically, we need to know: (a) predator–prey interaction strength (Heupel et al., 2014; Roff et al., 2016); (b) prey profitability (i.e. the energetic value of a prey item once prey digestive quality and time to chase, capture and handle prey have been considered; Fall & Fiksen, 2020; MacArthur & Pianka, 1966; Sih & Christensen, 2001), which is influenced by a variety of predator–prey tactics (Heithaus, 2004); and (3) the dispersal capabilities of both predator and prey.

2.2 | Using diet information to understand sympatric species coexistence

Research on resource partitioning can broaden our understanding of species coexistence within the same geographic locations (Schoener, 1974), and there is evidence that ray species partition their resources (Barría et al., 2015; Belleggia, Scenna, Barbini, Figueroa, & Díaz De Astarloa, 2014; Bornatowski, Wosnick, Do Carmo, Corrêa, & Abilhoa, 2014; Espinoza, Munroe, Clarke, Fisk, & Wehrmann, 2015; Every, Pethybridge, Fulton, Kyne, &

Crook, 2017; Navarro-González, Bohórquez-Herrera, Navia, & Cruz-Escalona, 2012; Pardo, Burgess, Teixeira, & Bennett, 2015; Plate II, Potter, & Clarke, 1998; Rastgoo et al., 2018; Shibuya, Araújo, & Zuanon, 2009; Silva-Garay, Pacheco, & Vélez-Zuazo, 2018; Stewart et al., 2017; Treloar, Laurie, Laurenson, & Stevens, 2007; Yemişken et al., 2018; Yick, Tracey, & White, 2011). For example, in Peru, the pygmy devil ray (*Mobula munkiana*, Mobulidae) had minimal isotopic niche overlap with three other devil ray species (*M. birostris*, *M. mobular* and *M. thurstoni*), which suggests that the pygmy devil ray may be feeding in a different area or on a different prey source than the other species (Stewart et al., 2017). In some cases, high dietary overlap was found among sympatric species, but differences in their preferred prey item were found (e.g. Brickle, Laptikhovsky, Pompert, & Bishop, 2003). At Ningaloo reef, dietary overlap between ray species was high and coexistence of these species may instead be driven by abundant resources or space partitioning (O'Shea, Thums, van Keulen, Kempster, & Meekan, 2013). Mechanisms of resource partitioning among rays also include differences in mouth morphology (Barbini & Lucifora, 2012; Rastgoo et al., 2018; Smale & Cowley, 1992), habitat use (Barbini & Lucifora, 2012; Plate II et al., 1998), behaviour (e.g. foraging tactics; Barbini & Lucifora, 2012; Rastgoo et al., 2018) and body size (Smale & Cowley, 1992). While competition is often the mechanism used to explain resource partitioning,

the link between the two has not been measured in ray field studies (Papastamatiou, Wetherbee, Lowe, & Crow, 2006; Schoener, 1974; Yick et al., 2011).

2.3 | Anti-predator behaviour by rays

Ray predators might influence ray behaviour, populations and ecological interactions through non-lethal mechanisms (Heithaus, 2004). Indeed, most animals invest in anti-predator behaviour (Lima & Dill, 1990). The probability of prey death via predation depends in part on avoidance tactics like hiding, aggregating, vigilance, escaping, defence and modifying activity levels and/or habitat use (Heithaus, 2004; Lima & Dill, 1990). While not thoroughly investigated, rays appear to be influenced by the risk of predation. Gastropods prey on skate egg cases (Cox & Koob, 1993; Cox, Walker, & Koob, 1999; Hoff, 2009; Lucifora & García, 2004; Smith & Griffiths, 1997) and the use of egg-case nurseries by skates (i.e. high densities of egg cases in a relatively small area) reduce predation rates (Hoff, 2009). In Shark Bay, Western Australia, whiprays (*Himantura* sp., Dasyatidae) respond faster to boat approaches (proxy for a predator) than cowtail rays (*Pastinachus sephen*, Dasyatidae), which suggests that the cowtail rays may benefit from grouping with whiprays that may detect predators sooner (Semeniuk & Dill, 2006). Whiprays and giant guitarfish (*Glaucostegus typus*, Glaucostegidae) rest in warm shallow water during the day in the warm season in Shark Bay, Western Australia, which corresponds with an increased abundance of tiger sharks and may be a refuging tactic (Vaudo & Heithaus, 2013). Resting in warm water suggests these rays likely incur metabolic costs, demonstrating that this behaviour is not consistent with behavioural thermoregulation (Vaudo & Heithaus, 2013). Other work has hypothesized that stingray activity, habitat use and/or movements may be driven at least in part by predation risk (e.g. Cartamil, Vaudo, Lowe, Wetherbee, & Holland, 2003; Cerutti-Pereyra et al., 2014; Davy, Simpfendorfer, & Heupel, 2015; Kanno, Schlaff, Heupel, & Simpfendorfer, 2019; Tilley, López-Angarita, & Turner, 2013b); however, none of these studies set out to test the effect of sharks on rays and alternative hypotheses could also explain the observed patterns (e.g. behavioural thermoregulation, interspecific competition, or prey density and distribution). Between 1970 and 2012 in the Gulf of St. Lawrence, Canada, thorny skates responded to an increase in grey seal (*Halichoerus grypus*, Phocidae) abundance by moving into lower risk areas in deeper waters (Swain, Benoît, & Hammill, 2015). It was hypothesized that since skate body condition is poor in deeper waters where they were refuging that skates exhibit a trade-off between foraging opportunities and safety (Swain et al., 2015). The foraging-safety trade-off is common among many taxa (Brown & Kotler, 2004; Lima & Dill, 1990). Caribbean reef sharks (*Carcharhinus perezi*, Carcharhinidae) in Belize may induce similar habitat shifts in southern stingrays because southern stingrays were seen more frequently on fished forereefs with low reef shark abundance than on protected forereefs with higher reef shark abundance (Bond et al., 2019). Additionally, southern stingrays on

the shallow sandflats spent more time at baited remote underwater video station (BRUVS) bait cages and had fewer injuries than southern stingrays in deeper forereef habitat where shark relative abundance was higher (Bond et al., 2019). Similar results were found using BRUVS across six countries in the western Pacific Ocean, where fewer small rays (*Neotrygon* spp. and *Taeniura* spp., Dasyatidae) were sighted in places where predatory shark and wedgefish abundance was high (Sherman, Heupel, Moore, Chin, & Simpfendorfer, 2020). Rays also spent more time in the video frame and were more likely to make feeding attempts on the bait bag where there were fewer predators (Sherman et al., 2020). This work highlights the need to consider mesopredator behaviour when looking for evidence of mesopredator release (Sherman et al., 2020). While existing evidence suggests that rays may modify habitat use and behaviour in response to predation risk, more studies that test a priori predictions and explicitly address alternative hypotheses are needed to understand the conditions under which predators shape ray anti-predator behaviour.

3 | CURRENT UNDERSTANDING OF RAY EFFECTS ON ECOSYSTEMS

3.1 | Potential impacts on prey densities

An overarching question in ray ecology is the degree to which their predator-prey interactions and disturbance of the benthos might affect prey population dynamics, community structure and ecosystem function. There are, however, limited empirical data to address these questions. For example, there are few studies that investigate if, and when, rays influence prey densities. Yet, this is an important area of study since rays have been blamed for declines in commercially important bivalves which have led to ray population control programs (Gray, Mulligan, & Hannah, 1997; Grubbs et al., 2016; Myers, Baum, Shepherd, Powers, & Peterson, 2007; Yamaguchi, Kawahara, & Ito, 2005). However, in many cases, rays were not actually important predators of bivalves (e.g. Bade, Balakrishnan, Pilgrim, McRae, & Luczkovich, 2014; Gray et al., 1997) and moratoria on ray hunting were instated, with managers pressing for further research (van Hees, Pien, Ebert, Cailliet, & Smith, 2015; Lloyd, 2017). While prey density thresholds can trigger ray feeding (Ajemian & Powers, 2013; Ajemian et al., 2012; Armstrong et al., 2016; Hines et al., 1997; Peterson, Fodrie, Summerson, & Powers, 2001; Takeuchi & Tamaki, 2014), our understanding of ray effects on prey populations remains limited to in situ experiments with varying results (Ajemian & Powers, 2013; Ajemian et al., 2012; Peterson et al., 2001; Peterson, Summerson, Prescott, & Fegley, 1989; Thrush, Pridmore, Hewitt, & Cummings, 1994). In North Carolina, initial work showed a decline in bay scallops (*Argopecten irradians*, Pectinidae) between October and December 1983, which coincided primarily with the arrival of herring gulls (*Larus argentatus*, Laridae) and ring-billed gulls (*Larus delawarensis*, Laridae; Peterson et al., 1989). The seagulls had a negative effect on bay scallop densities over a short time period at low tide on the shallow sandflat (Peterson

et al., 1989). The migration of American cownose rays (*Rhinoptera bonasus*, Rhinopteridae) occurs in August and early September, which did not overlap with the scallop decline (Peterson et al., 1989). In a field enclosure, small American cownose rays did not consume any tethered scallops over the course of six days, and scallop mortality was attributed to large whelks due to the lack of shell damage (Peterson et al., 1989). The seasonal decline of bay scallops was later attributed to adult American cownose rays because stockades prevented large rays from consuming mullet (*Mugilidae*) in a mesocosm, and the average number of recovered scallops from a ray enclosure field experiment was more than ten times the number of scallops collected from the control treatment that did not exclude rays (Peterson et al., 2001). However, the stockades may have also excluded other potential scallop predators (Grubbs et al., 2016), so it remains unclear whether the impact of American cownose rays was overestimated. Predator exclusion experiments in Manukau Harbour, New Zealand, revealed that bivalve (*Macromona liliana*, Tellinidae), crustacean (*Colurostylis lemurum*, Diastylidae), sea cucumber (*Taeniogyrus dendyi*, Chiridotidae) and ribbon worm (*Nemertea*) densities were negatively affected by New Zealand eagle ray and shorebird predation (Thrush et al., 1994). In contrast to this, polychaete (*Scoelepsis* sp., Spionidae and *Heteromastus filiformis*, Capitellidae) densities were positively influenced by eagle ray and shorebird predation (Thrush et al., 1994). While it was clear there was a combined negative effect of shorebird and eagle ray predation on the majority of infaunal prey densities, the effect of eagle rays alone was not estimated (Thrush et al., 1994). In Harrington Sound, Bermuda, calico clams (*Macrocallista maculata*, Veneridae) are the most abundant infauna and are the most important prey species in whitespotted eagle ray (*Aetobatus narinari*, Aetobatidae) diets (Ajemian et al., 2012). In an enclosure experiment with seeded calico clams in low, medium and high density patches, the proportional mortality rate of clams was similar across treatments, despite whitespotted eagle rays preferentially selecting high density patches (Ajemian et al., 2012). In Alabama, United States, an enclosure experiment demonstrated that American cownose rays did not impact amphipod densities (Ajemian & Powers, 2013). However, amphipods may have been replenished outside of the enclosures due to movement or sediment disturbance, hindering the team's ability to detect ray effects (Ajemian & Powers, 2013). A manipulative experiment demonstrated that blue crabs (*Callinectes sapidus*, Portunidae) were the primary source of hard clam (*Mercenaria* sp., Veneridae) mortality, not American cownose rays (Ajemian & Powers, 2013). In California, bat eagle rays (*Myliobatis californicus*, Myliobatidae) were the presumed cause of oyster declines; however, there was limited evidence of oysters in their diet and bat eagle rays are important predators of the red rock crab (*Cancer productus*, Cancridae), a species known to eat oysters (Gray et al., 1997). Predator and prey behaviour and life histories should also be considered when testing ray effects on prey density. Bivalves are able to emigrate in response to varying water flow regimes (Powers & Peterson, 2000) and predators (Peterson, Ambrose, & Hunt, 1982), while amphipods may reduce intraspecific competition through nocturnal activity (Hill, 1992). If prey growth is density independent, predators may smooth out prey distribution patterns and keep prey population levels near equilibrium.

Small-scale disturbances from ray feeding promote bivalve diversity, likely by prohibiting one species from becoming competitively dominant (Gaspie & Seitz, 2017). Impacts of rays on prey populations will also vary depending on whether the rays are resident or migratory. For example, the seasonal movements of American cownose rays may have a larger impact on bay scallop populations because the timing of predation precedes the autumn bay scallop spawning event (Peterson et al., 2001). The experimental results from various studies highlight that ray effects may be site-specific and influenced by experimental design. Therefore, caution should be taken prior to assuming that experimental results can be extended across large spatial scales (Grubbs et al., 2016). A deeper understanding of prey life history and spatiotemporal patterns in ray predation is needed to evaluate the potential impacts rays have on prey densities.

3.2 | Effects of direct predation and risk on wider community

Marine predators can have large impacts on their prey and ecosystems by inducing predator avoidance behaviour (e.g. Heithaus, Frid, Wirsing, & Worm, 2008; Madin, Dill, Ridlon, Heithaus, & Warner, 2016). Experimental work has demonstrated that rays might be able to affect benthic communities by altering the behaviour of their prey. For example, European green crabs (*Carcinus maenas*, Portunidae) limited their movements in the presence of smalleye skates (*Raja microocellata*, Rajidae), which led to a decrease in juvenile bivalve mortality when no mature blue mussel (*Mytilus edulis*, Mytilidae) beds were present (Barrios-O'Neill, Bertolini, & Collins, 2017). When mature mussel beds were present, bivalve mortality did not differ in the presence or absence of skates, demonstrating that benthic complexity can limit predator effects (Barrios-O'Neill et al., 2017). Another laboratory experiment showed that the invasive mussel (*Arcuatula senhousia*, Mytilidae) fed less in the presence of chemical cues of the native Haller's round ray (*Urobatis halleri*, Urotrygonidae; Castorani & Hovel, 2016). Both experiments reveal the potential for rays to influence the benthic environment as well as open water environments. A decrease in mussel filter feeding through vigilance or direct mortality could lead to changes in plankton abundance. In the wild, prey densities likely differ from experimental settings, and predation risk varies spatially and temporally (Lima & Bednekoff, 1999). Caution should be taken when considering experimental results, since effects from prey behavioural responses to predators are expected to be greater under acute risk (Lima & Bednekoff, 1999). However, these examples highlight that in some circumstances, rays may act as initiators of behaviourally mediated ecosystem interactions with outcomes that have the potential to extend beyond benthic environments.

A decline in apex predators can lead to an increase in the abundance of their prey, a phenomenon known as "mesopredator release" (Ritchie & Johnson, 2009). The depletion of apex species can then cause cascading effects through the ecosystem,

where their loss indirectly affects lower trophic levels via the increase and/or behavioural changes of mesopredators (Heithaus et al., 2008; Ritchie & Johnson, 2009). In order to demonstrate this empirically, ray abundance, distribution or behaviour would have to be driven by top-down processes and rays would have to be able to significantly impact benthic communities directly or indirectly. Evidence of ray release from apex predators has been documented in studies that rely primarily on species abundance and relative contribution to fisheries trends (Myers et al., 2007; Pradervand, Mann, & Bellis, 2007; Ward & Myers, 2005). For example, pelagic stingray (*Pteroplatytrygon violacea*, Dasyatidae) abundance increased in the tropical Pacific Ocean following a decline in top pelagic predators like sharks and tunas (Ward & Myers, 2005), and the relative contribution of ray catch in a South African recreational fishery increased following a decrease in the relative contribution of dusky (*Carcharhinus obscurus*, Carcharhinidae) and milk (*Rhizoprionodon acutus*, Carcharhinidae) shark catch (Pradervand et al., 2007). Another example presented evidence of a trophic cascade: a decline of predatory sharks due to fishing resulted in an increased abundance of several ray species including the American cownose ray and a subsequent decline in bay scallops (Myers et al., 2007). Recent work casts doubt on the described shark-mediated trophic cascade via direct predation exclusively (Grubbs et al., 2016). There remains a debate as to whether or not behaviour could be an explanatory mechanism for the patterns discovered by Myers et al. (2007). The negative effect of predation risk on prey populations can be as strong as direct predation alone (Peacor & Werner, 2000; Schmitz, Beckerman, & O'Brien, 1997), while risk effects and their interaction with direct predation can have larger effects on populations than direct predation alone (Creel & Christianson, 2008; Preisser, Bolnick, & Benard, 2005). Furthermore, predators need not affect the densities of prey populations to influence lower trophic levels through behavioural mechanisms (e.g. Creel & Christianson, 2008; Heithaus et al., 2008, 2010; Preisser et al., 2005). To date, the evidence that declining top predator abundance can lead to ray release is equivocal and warrants further investigation.

Trophic redundancy may increase food web complexity and could protect some systems from the negative effects of the loss of top predators as a type of biological insurance (Navia et al., 2016). A topological analysis suggested that in tropical networks the loss of one or more mesopredator ray species would not likely have an impact on overall system dynamics (Navia, Cortés, & Mejía-Falla, 2010). In contrast to this, a similar analysis in a subtropical food web proposed that the shortnose guitarfish (*Zapteryx brevirostris*, Trygonorrhinidae) is likely a central species in the network (Bornatowski, Navia, Braga, Abilhoa, & Corrêa, 2014). The difference in the relative importance of rays across the tropical and subtropical systems can be explained by latitude and species richness (Bornatowski, Navia, et al., 2014). Although topological models can be informative predictive tools, they assume that network parameters are random and that all species are interacting with one another, which does not accurately represent real world scenarios

(Proulx, Promislow, & Phillips, 2005). Discovering ways to incorporate environmental stochasticity and varying interaction strengths into network models has been identified as a priority in ecological function analysis (Brodie, Redford, & Doak, 2018). Many trophic models combine all rays and/or mesopredators into one category assuming high redundancy; however, moving forward it is important to understand how these groupings affect model ability to detect the consequences of changes in ray abundance (Navia et al., 2010; Ruocco & Lucifora, 2017). Similarly, lumping species without taking into account individual specializations may obscure important interactions (e.g. Bolnick et al., 2011).

3.3 | Bioturbation and nutrient dynamics

Rays are "bioturbators," a functional group that excavate and disturb sediments (e.g. Howard, Mayou, & Heard, 1977), which can lead to abiotic and biotic changes in the surrounding environment (Berke, 2010; Clifton & Hunter, 1973; Kogure & Wada, 2005; Laverock, Gilbert, Tait, Osborn, & Widdicombe, 2011; Meysman, Middelburg, & Heip, 2006). However, there is a paucity of information on the importance of small-scale ray disturbances to ecosystems. Bioturbation by rays can lead to high rates of sediment displacement (Takeuchi & Tamaki, 2014) and benthic disturbance that affects infaunal community structure (VanBlaricom, 1982). While spatial and temporal changes in sediment resuspension have been correlated with the abundance and activity of benthic fishes on several coral reefs in the Red Sea (Yahel, Yahel, & Genin, 2002), its implication for carbon sequestration and benthic oxygen cycling remains unclear (Yahel et al., 2008). Research that has explored the potential for nutrient accumulation inside feeding pits and community composition changes following ray bioturbation have come up with contrasting results (Table 2). Varying results across studies are likely due to differences in methodologies, locations and study species (Sherman, Reidenauer, Thistle, & Meeter, 1983; Thrush, Pridmore, Hewitt, & Cummings, 1991). The focus of recent research has been on the quantity of sediment turned over by rays, which does not clearly identify its importance to ecosystems, especially compared to other biogenic and physical processes. For example, as much as 42% of an intertidal area measuring $< 1 \text{ km}^2$ may be reworked annually due to bioturbation by broad cowtail rays (*Pastinachus ater*; Dasyatidae), whiprays (*Himantura* spp., Dasyatidae), porcupine whiprays (*Urogymnus asperrimus*; Dasyatidae) and bluespotted fantail rays (*Taeniura lymma*, Dasyatidae; O'Shea, Thums, van Keulen, & Meekan, 2012), while average daily sediment turnover rates by rays vary from $< 1\%$ (Grant, 1983) to 91% (Sherman et al., 1983). In Tomioka Bay, Japan, as many as 18,103 new pits were formed per day in an area $< 1 \text{ km}^2$ (Takeuchi & Tamaki, 2014), an estimate much greater than that in Manukau Harbour, New Zealand, where approximately 21 new pits were created per day in an area similar in size (Hines et al., 1997). Varying results may be due to ray density, body condition, behaviour (e.g. perceived risk in the area) and differences in methodologies across studies (e.g. pit measurements versus infilling pits with known sediment volumes). Relative to other biological and physical processes, especially tidal

sediment reworking, ray (Dasyatidae) bioturbation was not important on the Debidue Flat in South Carolina, USA (Grant, 1983). The pioneering work of VanBlaricom (1982) has, to our knowledge, not been replicated or built upon. This study focused on describing an infaunal community based on the effects of a multi-predator assemblage. This included testing the effects of ray disturbance on community structure, accumulation of organic matter and nutrient concentrations in pits, the subsequent recolonization of infauna into the pits and the potential importance of foraging opportunities for teleosts created by ray disturbance (Table 2).

Although the importance of ray bioturbation to nutrient dynamics remains understudied, it is likely important in many systems (Heithaus et al., 2010). Organic carbon (C) and organic nitrogen (N) accumulate at greater rates inside manufactured ray pits for at least 15 days compared to areas outside the pits (VanBlaricom, 1982). For example, the mean %C in ray pits after six days was 0.89 compared to 0.16 in control sites and the mean %N in ray pits after six days was 0.11 compared to 0.02 in control sites (VanBlaricom, 1982). The nutrient content in manufactured pits decreased over time, and no significant differences between pit and control site values were detected 37 days after pit creation (VanBlaricom, 1982). C:N ratios were only significantly different

between control sites and pits after six days (6.67 and 7.95, respectively; VanBlaricom, 1982). Ray movements across habitats may generate nutrient subsidies (Earl & Zollner, 2017) since foraging can take place in one habitat and excretion/egestion can occur in another. This may be the case for reef manta rays (*Mobula alfredi*, Mobulidae) that feed in the mesopelagic zone and move into shallow surface waters (Burgess et al., 2016), reef manta rays that travel between coral reef and pelagic ecosystems (Peel et al., 2019) and smalltooth sawfish that move from deep coastal to shallow mangrove habitats (Papastamatiou, Grubbs, et al., 2015). Additionally, large aggregations of rays, such as reef manta rays, may generate nutrient hotspots within specific areas given their propensity to exhibit philopatric behaviours (Peel et al., 2019). Fundamental to our understanding of these nutrient dynamics will be calculating the duration of ray feeding, egestion and excretion, which has only been done for Atlantic stingrays (*Hypanus sabinus*, Dasyatidae; Di Santo & Bennett, 2011). Rays themselves can be vectors of allochthonous resources. For example, ray carcasses provide a feeding opportunity in deep-sea environments (Higgs, Gates, & Jones, 2014). Scavengers feeding on three devil ray (Mobulidae) carcasses found at a depth > 1,000 m included eelpouts, hagfish, grenadiers, a skate and an eel; however, the community abundance around the carcasses

TABLE 2 Responses to small-scale ray feeding disturbances. Significant effects on response variables labelled as “–” (negative) or “+” (positive). Studies measuring only sedimentation rates by rays are not included, as the significance of turnover by rays compared to other processes was not tested

| Species | Location | Measured response variable(s) | Ray effect significant? | Section References |
|---|--|---|-----------------------------------|-----------------------------------|
| Atlantic stingray (<i>Hypanus sabinus</i> , Dasyatidae) | Saint George Sound, Florida, USA | Harpacticoid copepod community structure | No | Reidenauer and Thistle (1981) |
| Haller's round ray (<i>Urobatis halleri</i> , Urotrygonidae) | La Jolla, California, USA | Infauna community structure | Yes (varied response across taxa) | VanBlaricom (1982) |
| Bat eagle ray (<i>Myliobatis californicus</i> , Myliobatidae) | | Organic nitrogen and carbon concentrations | Yes (+) | |
| | | Organic matter accumulation | Yes (+) | |
| Stingrays (Dasyatidae) | Debidue Flat, South Carolina, USA | Sediment turnover relative to other biological and physical processes | No | Grant (1983) |
| Atlantic stingray | Saint George Sound, Florida, USA | Nematode community structure | No | Sherman et al. (1983) |
| New Zealand eagle ray (<i>Myliobatis tenuicaudatus</i> , Myliobatidae) | Manukau Harbour, North Island, New Zealand | Infauna community structure | No | Thrush et al. (1991) |
| | | Organic carbon concentration (bivalve dominated community) | No | |
| | | Organic carbon concentration (polychaete dominated community) | Yes (+) | |
| Stingrays (Dasyatidae) | Debidue Flat, South Carolina, USA | Dissolved oxygen concentration | Yes (–) | D'Andrea, Aller, and Lopez (2002) |
| | | Dissolved organic carbon | Yes (+) | |
| | | Organic matter accumulation | Yes (+) | |
| | | Advective porewater flux | Yes (–) | |
| American cownose rays (<i>Rhinoptera bonasus</i> , Rhinopteridae) | Chesapeake Bay, Virginia, USA | Thin-shelled deposit feeding bivalve density | Yes (–) | Glaspie and Seitz (2017) |
| | | Bivalve diversity | Yes (+) | |

did not compare to the high abundance of fauna around whale carcasses (Higgs et al., 2014). Despite this, the carbon input to an area of 1.23 km² by the devil ray carcasses and one whale shark (*Rhincodon typus*, Rhincodontidae) carcass accounted for approximately 4% of the daily particulate organic carbon flux (Higgs et al., 2014). In a shallow coastal system in Australia, a stingray carcass facilitated a unique in-faunal community, primarily nematode species indicative of anoxic environments (Fonseca, Hutchings, Vieira, & Gallucci, 2011).

3.4 | Facilitation and other symbiotic relationships

Foraging facilitation is a commensal relationship whereby ray activity enhances another species' ability to access food items (Boaden & Kingsford, 2012). Rays have been documented facilitating foraging for birds (Kajiura, Macesic, Meredith, Cocks, & Dirk, 2009) and numerous teleost taxa (breams [Nemipteridae; Boaden & Kingsford, 2012], characids [Characidae & Hemiodontidae; Neto & Carvalho, 2011], cobia [Rachycentridae; Smith & Merriner, 1982], flounders [Paralichthyidae; VanBlaricom, 1982], grunts [Hamulidae; Strand, 1988], jacks [Carangidae; Kiszka, Heithaus, & Quod, 2015], porcupinefish [Diodontidae; Strand, 1988], porgies [Sparidae; Strand, 1988] and wrasses [Labridae; Strand, 1988]). These interactions typically occur when rays search for prey, disturbing organisms that get released into the surrounding environment to become available for other predators. However, foraging facilitation may also manifest from other ray behaviours. For example, in Brazil Guiana dolphins (*Sotalia guianensis*; Delphinidae) feed on teleosts displaced from breaching giant manta rays (*Mobula birostris*, Mobulidae; Domit, Broadhurst, & Bornatowski, 2017). In La Jolla, California, speckled sanddabs (*Citharichthys stigmaeus*, Paralichthyidae) near pits dug by researchers along transects had a higher frequency of occurrence of several prey species in their stomach contents when compared with sanddab stomach contents in areas lacking disturbance (VanBlaricom, 1982). In order to understand the importance of foraging facilitation by rays for other taxa, net energy gain of associated species relative to other foraging options and other potential benefits need to be quantified.

Another symbiotic relationship involving rays includes "piggy-backing" or "hitchhiking," whereby organisms including octopus and pink whiprays (*Pateobatis fai*, Dasyatidae) have been observed using the back of stingrays to facilitate travel or reduce predation risk (Meekan, Trevitt, Simpfendorfer, & White, 2016; Souza, Ilarri, & Valentim, 2007). Remoras are often associated with megafauna including rays, and despite the potential benefits gained by both ray (e.g. removal of parasites [Ritter & Brunnenschweiler, 2003]) and remora (e.g. food acquisition, risk aversion and transportation [Norman, 1939; Ritter & Brunnenschweiler, 2003]) that would suggest a mutualistic relationship, there are hydrodynamic and body condition issues created by an attached remora (Beckert, Flammang, Anderson, & Nadler, 2016; Schwartz, 1977) that justify further investigation into the costs and benefits of attached remoras. Cleaning mutualisms also exist (Vaughan, Grutter, Costello, & Hutson, 2017), where southern stingrays and giant manta rays have been observed

displaying behavioural changes at cleaning stations to signal the cleaner fish (O'Shea, Kingsford, & Seymour, 2010; Snelson, Gruber, Murru, & Schmid, 1990). The relative importance of symbiotic interactions involving rays to populations of symbiotic species and community dynamics is unknown.

4 | ANTHROPOGENIC DRIVERS OF RAY ECOLOGY

4.1 | Predicting ray responses to climate change

The effects of anthropogenic climate change on ray ecology are still largely unknown and are likely to increase in the future. Vulnerability to climate change varies by species and will likely be exacerbated by multiple other stressors like development and fishing (Chin, Kyne, Walker, & McAuley, 2010), while in certain cases, climate change may have beneficial outcomes for rays. For example, little skate (*Leucoraja erinacea*, Rajidae) embryos exposed to higher CO₂ levels increased mineralization of crura and jaw cartilage, which may boost feeding performance (Di Santo, 2019). Direct effects of climate change on rays are those that are expected to alter physiological processes or life-history parameters. For example, little skate embryos from two different locations off the east coast of the United States (Georges Bank and the Gulf of Maine) had longer development times, higher metabolic costs, poor body condition and decreased survival when exposed experimentally to increased temperatures and acidification (Di Santo, 2015). However, the hatchlings from the two locations responded differently: the Georges Bank skates were smaller than the Gulf of Maine skates, suggesting that intraspecific responses to climate change will also vary depending on location (Di Santo, 2015). Smaller skates were healthier and less sensitive to acidification (Di Santo, 2015). Individual variation will affect how rays respond to climate change (e.g. Sih, Cote, Evans, Fogarty, & Pruitt, 2012). For example, individual Atlantic cod (*Gadus morhua*, Gadidae) with reactive personalities reduced their home range as temperature increased, while proactive (bold) individuals maintained their home range size or expanded it as waters warmed (Villegas-Ríos, Réale, Freitas, Moland, & Olsen, 2018). Bold personalities may be selected for under current predictions of global climate change (Villegas-Ríos et al., 2018). Ultimately, effect sizes will depend on the ability of species to adapt over longer periods of time that cannot be captured in laboratory experiments. Indirect effects of climate change on rays are those that are brought on by behavioural responses to altered habitats and species interactions. The most at-risk ray species in Australia live in freshwater and estuaries and will be impacted by saltwater intrusion due to sea level rise, warming water temperatures and increased storm intensity (e.g. porcupine whiprays and freshwater whiprays [*Urogyrnus dalyensis*, Dasyatidae; Chin et al., 2010]. Elasmobranchs use temperature to aid physiological processes (Di Santo & Bennett, 2011; Matern, Cech, & Hopkins, 2000; Papastamatiou, Watanabe, et al., 2015; Sims et al., 2006), and long-term changes in temperatures may alter ray behaviour. In the North

Sea, the cuckoo skate (*Leucoraja naevus*, Rajidae) moved into deeper water in response to increased temperatures, but its distribution did not change latitudinally (Perry, Low, Ellis, & Reynolds, 2005). Shifting habitats may mean rays incur fitness costs through the inability to find food, increased predation risk (e.g. Swain et al., 2015) and/or increased competition with other mesopredators. The cost of locomotion can be high at temperatures above species' thermal optima, and philopatric species may be disproportionately affected by warming water if their cost of transport is high (Lauder & Di Santo, 2015). For example, little skates have some of the highest costs of transport of any elasmobranch, measured by oxygen consumption rates, suggesting their ability to migrate in response to changing abiotic conditions may be limited (Di Santo & Kenaley, 2016). Further evidence supporting this is the decreased mineralization in the pectoral fin cartilage of little skate embryos exposed to increased temperatures, a direct effect of climate change, which may further increase the metabolic costs of locomotion and decrease their chances of moving into cooler refuges (Di Santo, 2019). The frequency and intensity of predator–prey interactions may be reshaped by climate change. For example, higher stress levels and poor body condition may limit rays' ability to seek refuge from predators, whose distributions may also be changing due to warming seas (e.g. Hazen et al., 2013). These examples highlight the need to combine behavioural and physiological research in order to predict ray species vulnerability to climate change.

4.2 | Fisheries impacts

Rays are subjected to both target and incidental fisheries around the world (Dulvy et al., 2014). At least 37% of all ray species (235 of 633 described) experience fishing pressure in some form (Table S5), and this estimate is highly conservative due to the lack of species-specific reporting (Bonfil, 1994; Curtis & Sosebee, 2015; De-Franco, Fernandes Mendonça, Oliveira, & Foresti, 2012; Dell'Apa, Kimmel, & Clò, 2012; Dulvy, Metcalfe, Glanville, Pawson, & Reynolds, 2000; Figueiredo et al., 2007; Machado, Gordo, & Figueiredo, 2004), the grouping of rays in fishery data (Moore, McCarthy, Carvalho, & Peirce, 2012; Silva, Ellis, & Catchpole, 2012) and the use of only primary literature in this review. Large sawfishes (Pristidae) have been completely eradicated in many places and undergone severe range restrictions due to fishing (e.g. Dulvy et al., 2016). Similar local extinctions of skates have occurred, for example, commercial fishing in the northwest Black Sea led to the disappearance of the common stingray (*Dasyatis pastinaca*, Dasyatidae) and the thornback skate in the early 2000s, which consequently led to food webs with fewer trophic links and connectivity (Bănuș, Harmelin-Vivien, & Boudouresque, 2010). Declines in large skate species due to commercial fishing are well documented (e.g. Bănuș et al., 2010; Brander, 1981) and in some cases induced community shifts because of competitive release (Agnew, Nolan, Beddington, & Baranowski, 2000; Dulvy et al., 2000; Ruocco, Lucifora, Díaz de Astarloa, & Menni, 2012;

Walker & Heessen, 1996). When large species decline, smaller species may be released from interspecies competition and take over the niche of larger species (Dulvy et al., 2000; Ruocco et al., 2012). Declining predator abundance affects rays directly and indirectly (e.g. Bond et al., 2019; Ward & Myers, 2005), and until we gain a clearer understanding of ray impacts on prey populations and nutrient dynamics, it is difficult to predict ecosystem level consequences of ray declines. Trawling threatens rays directly because they are by-catch, but also indirectly through the depletion of prey sources like shrimp or changes in demersal prey species assemblages (e.g. Espinoza et al., 2015). Since many rays are generalists, measuring the effect of prey declines on ray populations will likely be challenging as rays may simply switch to other prey taxa. This could lead to increased intra- and interspecific competition. With tremendous impacts to populations of rays, their predators and their prey and wider impacts on ecosystems, the contribution of fisheries to ray ecology cannot be overlooked.

4.3 | Interactions with tourism

Elasmobranch tourism benefits national economies (Brunnschweiler, 2010; Haas et al., 2017; O'Malley et al., 2013; Topelko & Dearden, 2005; Vaudo et al., 2018), and the economic importance of rays to tourism industries has contributed to several successful conservation initiatives (e.g. "Belize Fisheries Resources Act", 2020; Cayman Islands, 2013; Ward-Paige, 2017). Although tourism is often promoted as an alternative to fishing (Gallagher et al., 2015), left unmanaged it can have deleterious cascading effects on ecosystems (e.g. Ripple & Beschta, 2006). Tourism is also linked to recreational fisheries, but these fisheries have remained relatively understudied from a tourism perspective (Borch, Policansky, & Aas, 2008). Of primary concern for most ray tourism operations is the potential for overcrowding (O'Malley et al., 2013). Provisioning is a common practice that entices rays to come close to boats and tourists (Corcoran et al., 2013; Gaspar, Chateau, & Galzin, 2008; Lewis & Newsome, 2003; Newsome, Lewis, & Moncrieff, 2004) and also occurs when fishers clean their catch (Pini-Fitzsimmons, Knott, & Brown, 2018). Provisioning can lead to increased density at the feeding site (Corcoran et al., 2013), reverse normal diel stingray activity (Corcoran et al., 2013; Shackley, 1998), cause some individuals to exhibit anticipatory behaviour (Gaspar et al., 2008; Pini-Fitzsimmons et al., 2018), lead to aggression between individuals (Newsome et al., 2004), increase parasite loads (Semeniuk & Rothley, 2008) and negatively influence body condition (Semeniuk, Bourgeon, Smith, & Rothley, 2009; Semeniuk & Rothley, 2008; Semeniuk, Speers-Roesch, & Rothley, 2007). Higher boat traffic to tourism hotspots may also increase the chance of vessel strikes on rays (McGregor, Richardson, Armstrong, Armstrong, & Dudgeon, 2019). Concentration of individuals into small areas may lead to higher competition for food and attract predators. The latter would be particularly concerning for smaller individuals who may be in poor body condition resulting from competitive conflict and not have the energy to invest in

anti-predator behaviour. Provisioning likely also reduces pressure on nearby prey populations, and may reduce sediment turnover rates. Hypothesis-driven research is needed to understand how and when tourism could have ecosystem level effects. Management strategies are the ideal way to ensure sustainable and responsible tourism practices, such as working with and respecting Indigenous communities, limiting the number of tourists per site visit, controlling the type and amount of food offered daily and enforcing a minimum human or boat to ray distance (Lawrence et al., 2016).

5 | CONCLUSION AND PATH FORWARD

There is a wealth of literature on broad topics in ray ecology, yet there remains ample opportunity to assess the importance of rays to community dynamics and ecosystem function. While we have a basic understanding of ray trophic roles and interactions with their environment, our knowledge on the relative strength and importance of species and habitat interactions is limited and often based on speculative hypotheses derived from manipulative experiments or studies with goals that were not focused on addressing the ecological importance of rays. The need to resolve species complexes and address the lack of basic biological information for many ray species hinders our ability to grapple with more elaborate ecological questions. We urge scientists to focus on hypothesis-driven research in order to gain a better understanding of ray ecological roles and importance. Attention should be focused on three key areas, while attempting to measure ultimate, rather than proximate response variables (Table 3; Brodie et al., 2018):

1. *Ray effects on prey:* There are many studies describing ray diets, yet we are still lacking a broad understanding of which species are true prey specialists. Given the occurrence of conspecific and congeneric predation by rays, research should clarify whether this type of predation is occurring in order to reduce competition among sympatric species or whether it results simply from being a generalist feeder. The role rays play in structuring prey populations, and potentially, whole ecosystems remain open to interpretation based on conflicting results across studies. This underpins the value of considering both consumptive and non-consumptive effects when studying prey responses to changes in ray abundance. It has been largely assumed that rays have a negative effect on prey densities, and research has yet to reach a consensus regarding this hypothesis. The impact of ray foraging on prey densities is expected to be influenced by a variety of factors including the presence of potential ray predators and competitors as well as ray movements (migratory or philopatric). Prey responses will likely be species-specific and based on life-history parameters (e.g. growth rates) as well as escape tactics. Preliminary experiments suggest that crabs and bivalves are able to respond behaviourally to perceived risk (e.g. Barrios-O'Neill et al., 2017; Castorani & Hovel, 2016), which may have the potential to affect ecosystem dynamics.

2. *Predator effects on rays:* Future research examining trophic relationships should attempt to understand the relative importance of rays to predator diets. Apex predator size classes are the most likely to exhibit concentrated predation and thus exert top-down effects on mesopredators (Heupel et al., 2014). The extent to which mesopredator (ray) release occurs following the decline of top predators is unresolved and warrants further investigation. There is no doubt that rays respond to perceived predation risk (e.g. Bond et al., 2019; Swain et al., 2015), but it will be important to measure the effects of predation risk on ecosystem dynamics and prey population growth rates rather than prey behavioural responses alone (e.g. habitat shifts) in order to gain a thorough understanding of how risk effects may cascade through ecosystems (Table 3). Mathematical predictions suggest that risk effects can stabilize prey populations, promote predator-prey coexistence and reduce the spread of disease in prey populations (Sarkar & Khajanchi, 2020; Sha, Samanta, Martcheva, & Chattopadhyay, 2019). Prey with high growth rates may also be less sensitive to risk effects (Sarkar & Khajanchi, 2020). Empirical testing of these predictions should be prioritized in order to identify the conditions under which top-down effects will be beneficial or detrimental to ray populations.
3. *Nutrient dynamics:* While rays are bioturbators, our understanding of this process' importance is limited as many studies focus on measuring proximate response variables alone (i.e. amount of sediment disturbed by rays across small areas, measured through pit volume and density). Ultimately, we want to gain an understanding of how bioturbation by rays may affect community structure and ecosystem productivity (Table 3). In other words, our focus should be on measuring the importance of nutrient release from ray bioturbation to surrounding communities (e.g. seagrass, coral reef), rather than simply how much sediment is turned over in a particular area over time. The presumed benefits of bioturbation via foraging facilitation also require further investigation, which could include comparing the diet of ray attendant species in areas where rays are present and areas where rays are absent. Movement ecology and physiology will provide insight on active subsidy transfer (movement of nutrients across ecosystems) by rays and the extent to which these processes affect ecosystem function (Earl & Zollner, 2017).

While our recommendations to measure ultimate response variables should serve as a guide to test ecological theory (Table 3), we recognize that this list is not exhaustive. A thorough comprehension of predator-prey interactions will require combining trophic information with behavioural and life-history data. We emphasize the need to move past basic diet descriptions and measurements of ray sediment turnover towards behavioural experiments and quantifying the importance of rays to the maintenance of ecosystem function and structure. Otherwise, our knowledge of the ecological roles and importance of rays may remain buried in the sand.

TABLE 3 Ecological functions involving rays and the identification of proximate and ultimate response variables. While measuring proximate response variables can be informative, in order to determine the importance of rays to ecosystems, research questions should be developed that seek to measure ultimate response variables. Constructed based off Brodie et al., 2018

| Function | Independent variable(s) | Proximate response variable(s) | Ultimate response variable(s) |
|---|--------------------------------|--|---|
| Bioturbation | Ray density | Pit density | Infauna community density |
| | | Pit volume | Infauna community structure |
| | | Nutrient release | Ecosystem change |
| | | Sediment turnover rates | Ecosystem productivity |
| Nutrient transport | Ray movements between habitats | Nutrient transport rates | Ecosystem productivity |
| | Ray carcass density | | |
| Predation on rays | Predator density | Ray density | Primary consumer density Primary consumer diversity |
| Predation by rays | Ray density | Prey density | Detritus accumulation |
| | | | Infauna community structure |
| | | | Plankton concentrations |
| Predator avoidance by rays and their prey | Perceived risk | Predator density | Prey fitness |
| | | Predator-prey spatiotemporal overlap | Prey population growth rates |
| | | Predator avoidance tactics | Ecosystem change Ecosystem productivity |
| Foraging facilitation | Ray density | Follow rates by attendant species | Importance of prey items excavated by rays to attendant species |
| | | Consumption rates by attendant species | |

ACKNOWLEDGEMENTS

This work was supported by the Mays Family Foundation. This is contribution #213 from the Coastlines and Oceans Division of the Institute of Environment at Florida International University. We gratefully acknowledge Demian Chapman and Jeremy Kiszka for useful discussions regarding this manuscript. We would also like to thank the editor and two reviewers for their helpful comments that improved this manuscript.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study. The information that is presented was synthesized from published literature using Google Scholar (<https://scholar.google.ca>).

ORCID

Kathryn I. Flowers  <https://orcid.org/0000-0002-4354-2948>

Michael R. Heithaus  <https://orcid.org/0000-0002-3219-1003>

Yannis P. Papastamatiou  <https://orcid.org/0000-0002-6091-6841>

REFERENCES

- Abdurahiman, K. P., Nayak, T. H., Zacharia, P. U., & Mohamed, K. S. (2010). Trophic organisation and predator-prey interactions among commercially exploited demersal finfishes in the coastal waters of the southeastern Arabian Sea. *Estuarine, Coastal and Shelf Science*, 87(4), 601–610. <https://doi.org/10.1016/j.ecss.2010.03.002>
- Agnew, D. J., Nolan, C. P., Beddington, J. R., & Baranowski, R. (2000). Approaches to the assessment and management of multispecies skate and ray fisheries using the Falkland Islands fishery as an example. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(2), 429–440. <https://doi.org/10.1139/f99-294>
- Ajayi, T. O. (1982). Food and feeding habits of *Raja* species (Batoidei) in Carmarthen Bay, Bristol Channel. *Journal of the Marine Biological Association of the UK*, 62(1), 215–223.
- Ajemian, M. J., & Powers, S. P. (2013). Foraging effects of cownose rays (*Rhinoptera bonasus*) along barrier islands of the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology*, 439, 119–128. <https://doi.org/10.1016/j.jembe.2012.10.021>
- Ajemian, M. J., Powers, S. P., & Murdoch, T. J. T. (2012). Estimating the potential impacts of large mesopredators on benthic resources: Integrative assessment of spotted eagle ray foraging ecology in Bermuda. *PLoS One*, 7(7), e40227. <https://doi.org/10.1371/journal.pone.0040227>
- Armstrong, A. O., Armstrong, A. J., Jaine, F. R. A., Couturier, L. I. E., Fiora, K., Uribe-Palomino, J., ... Richardson, A. J. (2016). Prey density threshold and tidal influence on reef manta ray foraging at an aggregation site on the Great Barrier Reef. *PLoS One*, 11(5), e0153393. <https://doi.org/10.1371/journal.pone.0153393>
- Aschliman, N. C., Nishida, M., Miya, M., Inoue, J. G., Rosana, K. M., & Naylor, G. J. P. (2012). Body plan convergence in the evolution of skates and rays (Chondrichthyes: Batoidea). *Molecular Phylogenetics and Evolution*, 63(1), 28–42. <https://doi.org/10.1016/j.ympev.2011.12.012>
- Bade, L. M., Balakrishnan, C. N., Pilgrim, E. M., McRae, S. B., & Luczkovich, J. J. (2014). A genetic technique to identify the diet of cownose rays, *Rhinoptera bonasus*: Analysis of shellfish prey items from North Carolina and Virginia. *Environmental Biology of Fishes*, 97(9), 999–1012. <https://doi.org/10.1007/s10641-014-0290-3>

- Bănar, D., Harmelin-Vivien, M., & Boudouresque, C. F. (2010). Man induced change in community control in the north-western Black Sea: The top-down bottom-up balance. *Marine Environmental Research*, 69(4), 262–275. <https://doi.org/10.1016/j.marenvres.2009.11.009>
- Barbini, S. A., & Lucifora, L. O. (2011). Feeding habits of the Rio skate, *Rioraja agassizi* (Chondrichthyes: Rajidae), from off Uruguay and north Argentina. *Journal of the Marine Biological Association of the United Kingdom*, 91(6), 1175–1184. <https://doi.org/10.1017/S0025315410001529>
- Barbini, S. A., & Lucifora, L. O. (2012). Ontogenetic diet shifts and food partitioning between two small sympatric skates (Chondrichthyes, Rajidae) in the Southwestern Atlantic. *Marine and Freshwater Research*, 63(10), 905–913. <https://doi.org/10.1071/MF12131>
- Barbini, S. A., & Lucifora, L. O. (2016). Big fish (and a smallish skate) eat small fish: Diet variation and trophic level of *Sympterygia acuta*, a medium-sized skate high in the food web. *Marine Ecology*, 37(2), 283–293. <https://doi.org/10.1111/maec.12273>
- Barria, C., Coll, M., & Navarro, J. (2015). Unravelling the ecological role and trophic relationships of uncommon and threatened elasmobranchs in the western Mediterranean Sea. *Marine Ecology Progress Series*, 539, 225–240. <https://doi.org/10.3354/meps11494>
- Barrios-O'Neill, D., Bertolini, C., & Collins, P. C. (2017). Trophic cascades and the transient keystone concept. *Biological Conservation*, 212, 191–195. <https://doi.org/10.1016/j.biocon.2017.06.011>
- Beckert, M., Flammang, B. E., Anderson, E. J., & Nadler, J. H. (2016). Theoretical and computational fluid dynamics of an attached remora (*Echeneis naucrates*). *Zoology*, 119, 430–438. <https://doi.org/10.1016/j.zool.2016.06.004>
- Belize Fisheries Resources Act (2020). *Publication No. 7*. Retrieved from <https://www.nationalassembly.gov.bz/wp-content/uploads/2020/03/Act-No.-7-of-2020-Fisheries-Resources-Act.pdf>
- Belleggia, M., Andrada, N., Paglieri, S., Cortés, F., Massa, A. M., Figueroa, D. E., & Bremec, C. (2016). Trophic ecology of yellownose skate *Zearaja chilensis*, a top predator in the south-western Atlantic Ocean. *Journal of Fish Biology*, 88, 1070–1087. <https://doi.org/10.1111/jfb.12878>
- Belleggia, M., Mabrugaña, E., Figueroa, D. E., Scenna, L. B., Barbini, S. A., & Díaz De Astarloa, J. M. (2008). Food habits of the broad nose skate, *Bathyraja brachyurops* (Chondrichthyes, Rajidae), in the south-west Atlantic. *Scientia Marina*, 72(4), 701–710. <https://doi.org/10.3989/scimar.2008.72n4701>
- Belleggia, M., Scenna, L. B., Barbini, S. A., Figueroa, D. E., & Díaz De Astarloa, J. M. (2014). The diets of four *Bathyraja* skates (Elasmobranchii, Arhynchobatidae) from the Southwest Atlantic. *Cybius*, 38(4), 314–318.
- Berke, S. K. (2010). Functional groups of ecosystem engineers: A proposed classification with comments on current issues. *Integrative and Comparative Biology*, 50(2), 147–157. <https://doi.org/10.1093/icb/icq077>
- Blanco-Parra, M. D. P., Galván-Magaña, F., Márquez-Farías, J. F., & Niño-Torres, C. A. (2012). Feeding ecology and trophic level of the banded guitarfish, *Zapteryx exasperata*, inferred from stable isotopes and stomach content analysis. *Environmental Biology of Fishes*, 95, 65–77. <https://doi.org/10.1007/s10641-011-9862-7>
- Boaden, A. E., & Kingsford, M. J. (2012). Diel behaviour and trophic ecology of *Scolopsis bilineatus* (Nemipteridae). *Coral Reefs*, 31(3), 871–883. <https://doi.org/10.1007/s00338-012-0903-2>
- Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., ... Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26(4), 183–192. <https://doi.org/10.1016/j.tree.2011.01.009>
- Bond, M. E., Valentin-Albanese, J., Babcock, E. A., Heithaus, M. R., Grubbs, R. D., Cerrato, R., ... Chapman, D. D. (2019). Top predators induce habitat shifts in prey within marine protected areas. *Oecologia*, 190(2), 375–385. <https://doi.org/10.1007/s00442-019-04421-0>
- Bonfil, R. (1994). *Overview of world elasmobranch fisheries*. FAO Fisheries Technical Paper 341. Rome: Food and Agriculture Organization of the United Nations. Retrieved from <http://www.fao.org/3/V3210E/V3210E00.htm>
- Bonfil, R., Ricaño-Soriano, M., Mendoza-Vargas, O. U., Méndez-Loeza, I., Pérez-Jiménez, J. C., Bolaño-Martínez, N., & Palacios-Barreto, P. (2018). Tapping into local ecological knowledge to assess the former importance and current status of sawfishes in Mexico. *Endangered Species Research*, 36, 213–228. <https://doi.org/10.3354/esr00899>
- Borch, T., Policansky, D., & Aas, Ø. (2008). International fishing tourism: Past, present and future. In Ø. Aas (Ed.), *Global challenges in recreational fisheries* (pp. 268–291). Oxford, UK: Blackwell Publishing Ltd.
- Bornatowski, H., Navia, A. F., Braga, R. R., Abilhoa, V., & Corrêa, M. F. M. (2014). Ecological importance of sharks and rays in a structural foodweb analysis in southern Brazil. *ICES Journal of Marine Science*, 71(7), 1586–1592. <https://doi.org/10.1093/icesjms/fsu025>
- Bornatowski, H., Robert, M. C., & Costa, L. (2010). Feeding of guitarfish *Rhinobatos percellens* (Walbaum, 1972) (Elasmobranchii, Rhinobatidae), the target of artisanal fishery in Southern Brazil. *Brazilian Journal of Oceanography*, 58(1), 45–52. <https://doi.org/10.1590/s1679-87592010000100005>
- Bornatowski, H., Wosnick, N., Do Carmo, W. P. D., Corrêa, M. F. M., & Abilhoa, V. (2014). Feeding comparisons of four batoids (Elasmobranchii) in coastal waters of southern Brazil. *Journal of the Marine Biological Association of the United Kingdom*, 94(7), 1491–1499. <https://doi.org/10.1017/S0025315414000472>
- Borrell, A., Cardona, L., Kumarran, R. P., & Aguilar, A. (2011). Trophic ecology of elasmobranchs caught off Gujarat, India, as inferred from stable isotopes. *ICES Journal of Marine Science*, 68, 547–554. <https://doi.org/10.1093/icesjms/fsq170>
- Braccini, J. M., & Perez, J. E. (2005). Feeding habits of the sand skate *Psammobatis extenta* (Garman, 1913): Sources of variation in dietary composition. *Marine and Freshwater Research*, 56(4), 395–403. <https://doi.org/10.1071/MF04205>
- Branco-Nunes, I. S. L., Albuquerque, F. V., Nunes, D. M., Oliveira, P. G. V., & Hazin, F. H. V. (2016). First record of predation between *Dasyatis* species. *Journal of Fish Biology*, 89(4), 2178–2181. <https://doi.org/10.1111/jfb.13091>
- Brander, K. (1981). Disappearance of common skate *Raja batis* from Irish Sea. *Nature*, 290(5801), 48–49.
- Bräutigam, A., Callow, M., Campbell, I. R., Camhi, M. D., Cornish, A. S., Dulvy, N. K., ... Welch, D. J. (2015). *Global priorities for conserving sharks and rays: A 2015–2025 strategy*. Retrieved from http://www.sharkadvocates.org/pdf/gsri_globalprioritiesforconservingsharksandrays_2-16.pdf
- Brickle, P., Laptikhovsky, V., Pompert, J., & Bishop, A. (2003). Ontogenetic changes in the feeding habits and dietary overlap between three abundant rajid species on the Falkland Islands' shelf. *Journal of the Marine Biological Association of the United Kingdom*, 83(5), 1119–1125. <https://doi.org/10.1017/S0025315403008373h>
- Brodie, J. F., Redford, K. H., & Doak, D. F. (2018). Ecological function analysis: Incorporating species roles into conservation. *Trends in Ecology & Evolution*, 33(11), 840–850. <https://doi.org/10.1016/j.tree.2018.08.013>
- Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, 7(10), 999–1014. <https://doi.org/10.1111/j.1461-0248.2004.00661.x>
- Brown, S. C., Bizzarro, J. J., Cailliet, G. M., & Ebert, D. A. (2012). Breaking with tradition: Redefining measures for diet description with a case study of the Aleutian skate *Bathyraja aleutica* (Gilbert 1896). *Environmental Biology of Fishes*, 95(1), 3–20. <https://doi.org/10.1007/s10641-011-9959-z>

- Brunnschweiler, J. M. (2010). The Shark Reef Marine Reserve: A marine tourism project in Fiji involving local communities. *Journal of Sustainable Tourism*, 18(1), 29–42. <https://doi.org/10.1080/09669580903071987>
- Burgess, K. B., Couturier, L. I. E., Marshall, A. D., Richardson, A. J., Weeks, S. J., & Bennett, M. B. (2016). *Manta birostris*, predator of the deep? Insight into the diet of the giant manta ray through stable isotope analysis. *Royal Society Open Science*, 3, 160717. <https://doi.org/10.1098/rsos.160717>
- Cartamil, D. P., Vaudo, J. J., Lowe, C. G., Wetherbee, B. M., & Holland, K. N. (2003). Diel movement patterns of the Hawaiian stingray, *Dasyatis lata*: Implications for ecological interactions between sympatric elasmobranch species. *Marine Biology*, 142(5), 841–847. <https://doi.org/10.1007/s00227-003-1014-y>
- Castorani, M. C. N., & Hovel, K. A. (2016). Native predator chemical cues induce anti-predation behaviors in an invasive marine bivalve. *Biological Invasions*, 18(1), 169–181. <https://doi.org/10.1007/s10530-015-1000-6>
- Cayman Islands (2013). *Marine conservation law*. Retrieved from <http://extwprlegs1.fao.org/docs/pdf/cay100292.pdf>
- Cerutti-Pereyra, F., Thums, M., Austin, C. M., Bradshaw, C. J. A., Stevens, J. D., Babcock, R. C., ... Meekan, M. G. (2014). Restricted movements of juvenile rays in the lagoon of Ningaloo Reef, Western Australia—evidence for the existence of a nursery. *Environmental Biology of Fishes*, 97(4), 371–383. <https://doi.org/10.1007/s10641-013-0158-y>
- Chin, A., Kyne, P. M., Walker, T. I., & McAuley, R. B. (2010). An integrated risk assessment for climate change: Analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. *Global Change Biology*, 16(7), 1936–1953. <https://doi.org/10.1111/j.1365-2486.2009.02128.x>
- Cliff, G. (1995). Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 8. The great hammerhead shark *Sphyrna mokarran* (Rüppell). *South African Journal of Marine Science*, 15(1), 105–114. <https://doi.org/10.2989/025776195784156331>
- Clifton, H. E., & Hunter, R. E. (1973). Bioturbational rates and effects in carbonate sand, St. John, US Virgin Islands. *The Journal of Geology*, 81(3), 253–268.
- Coll, M., Navarro, J., & Palomera, I. (2013). Ecological role, fishing impact, and management options for the recovery of a Mediterranean endemic skate by means of food web models. *Biological Conservation*, 157, 108–220. <https://doi.org/10.1016/j.biocon.2012.06.029>
- Corcoran, M. J., Wetherbee, B. M., Shivji, M. S., Potenski, M. D., Chapman, D. D., & Harvey, G. M. (2013). Supplemental feeding for ecotourism reverses diel activity and alters movement patterns and spatial distribution of the southern stingray, *Dasyatis americana*. *PLoS One*, 8(3), e59235. <https://doi.org/10.1371/journal.pone.0059235>
- Costa, T. L. A., Thayer, J. A., & Mendes, L. F. (2015). Population characteristics, habitat and diet of a recently discovered stingray *Dasyatis marianae*: Implications for conservation. *Journal of Fish Biology*, 86, 527–543. <https://doi.org/10.1111/jfb.12572>
- Cox, D. L., & Koob, T. J. (1993). Predation on elasmobranch eggs. *Environmental Biology of Fishes*, 38, 117–125. <https://doi.org/10.1007/BF00842908>
- Cox, D. L., Walker, P., & Koob, T. J. (1999). Predation on eggs of the thorny skate. *Transactions of the American Fisheries Society*, 128, 380–384. [https://doi.org/10.1577/1548-8659\(1999\)128<0380:POEOT>2.0.CO;2](https://doi.org/10.1577/1548-8659(1999)128<0380:POEOT>2.0.CO;2)
- Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, 23(4), 194–201. <https://doi.org/10.1016/j.tree.2007.12.004>
- Curtis, T. H., & Sosebee, K. A. (2015). Landings composition of the Northeast U.S. skate, Rajidae, wing fishery and the effectiveness of prohibited species regulations. *Marine Fisheries Review*, 77(4), 1–8. <https://doi.org/10.7755/MFR.77.4.1>
- D'Alberto, B. M., White, W. T., Chin, A., & Simpfendorfer, C. A. (2019). Untangling the Indonesian tangle net fishery: Describing a data-poor fishery targeting large threatened rays (Order Batoidea). *bioRxiv*, 608935.
- D'Andrea, A. F., Aller, R. C., & Lopez, G. R. (2002). Organic matter flux and reactivity on a South Carolina sandflat: The impacts of porewater advection and microbiological structures. *Limnology and Oceanography*, 47(4), 1056–1070. <https://doi.org/10.4319/lo.2002.47.4.1056>
- Dale, J. J., Wallsgrove, N. J., Popp, B. N., & Holland, K. N. (2011). Nursery habitat use and foraging ecology of the brown stingray *Dasyatis lata* determined from stomach contents, bulk and amino acid stable isotopes. *Marine Ecology Progress Series*, 433, 221–236. <https://doi.org/10.3354/meps09171>
- Davy, L. E., Simpfendorfer, C. A., & Heupel, M. R. (2015). Movement patterns and habitat use of juvenile mangrove whiprays (*Himantura granulata*). *Marine and Freshwater Research*, 66(6), 481–492. <https://doi.org/10.1071/MF14028>
- de la Rosa-Meza, K., Sosa-Nishizaki, O., & de la Dueva-Salcedo, H. (2013). Feeding habits of the speckled guitarfish *Rhinobatos glaucostigma* (Elasmobranchii, Batoidea) in the southeastern Gulf of California. *Ciencias Marinas*, 39(3), 277–290. <https://doi.org/10.7773/cm.v39i3.2229>
- Dean, M. N., Bizzarro, J. J., Clark, B., Underwood, C. J., & Johanson, Z. (2017). Large batoid fishes frequently consume stingrays despite skeletal damage. *Royal Society Open Science*, 4, 170674. <https://doi.org/10.1098/rsos.170674>
- De-Franco, B. A., Fernandes Mendonça, F., Oliveira, C., & Foresti, F. (2012). Illegal trade of the guitarfish *Rhinobatos horkelii* on the coasts of central and southern Brazil: Genetic identification to aid conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22, 272–276. <https://doi.org/10.1002/aqc.2229>
- Dell'Apa, A., Kimmel, D. G., & Clò, S. (2012). Trends of fish and elasmobranch landings in Italy: Associated management implications. *ICES Journal of Marine Science*, 69(6), 1045–1052. <https://doi.org/10.1093/icesjms/fss067>
- Delpiani, G. E., Spath, M. C., & Figueroa, D. E. (2013). Feeding ecology of the southern thorny skate, *Amblyraja doellojuradoi* on the Argentine Continental Shelf. *Journal of the Marine Biological Association of the United Kingdom*, 93(8), 2207–2216. <https://doi.org/10.1017/S0025315413000787>
- Di Santo, V. (2015). Ocean acidification exacerbates the impacts of global warming on embryonic little skate, *Leucoraja erinacea* (Mitchill). *Journal of Experimental Marine Biology and Ecology*, 463, 72–78. <https://doi.org/10.1016/j.jembe.2014.11.006>
- Di Santo, V. (2019). Ocean acidification and warming affect skeletal mineralization in a marine fish. *Proceedings of the Royal Society B*, 286(1894), 20182187. <https://doi.org/10.1098/rspb.2018.2187>
- Di Santo, V., & Bennett, W. A. (2011). Is post-feeding thermotaxis advantageous in elasmobranch fishes? *Journal of Fish Biology*, 78(1), 195–207. <https://doi.org/10.1111/j.1095-8649.2010.02853.x>
- Di Santo, V., & Kenaley, C. P. (2016). Skating by: Low energetic costs of swimming in a batoid fish. *Journal of Experimental Biology*, 219(12), 1804–1807. <https://doi.org/10.1242/jeb.136358>
- Domit, C., Broadhurst, M. K., & Bornatowski, H. (2017). Interactions between *Manta birostris* and *Sotalia guianensis* in a World Heritage listed Brazilian estuary. *Journal of Fish Biology*, 91(4), 1236–1240. <https://doi.org/10.1111/jfb.13399>
- Dulvy, N. K., Davidson, L. N., Kyne, P. M., Simpfendorfer, C. A., Harrison, L. R., Carlson, J. K., & Fordham, S. V. (2016). Ghosts of the coast: Global extinction risk and conservation of sawfishes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26(1), 134–153. <https://doi.org/10.1002/aqc.2525>
- Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., ... White, W. T. (2014). Extinction risk and conservation of the world's sharks and rays. *eLife*, 3, e00590. <https://doi.org/10.7554/eLife.00590>

- Dulvy, N. K., Metcalfe, J. D., Glanville, J., Pawson, M. G., & Reynolds, J. D. (2000). Fishery stability, local extinctions, and shifts in community structure in skates. *Conservation Biology*, 14(1), 283–293. <https://doi.org/10.1046/j.1523-1739.2000.98540.x>
- Earl, J. E., & Zollner, P. A. (2017). Advancing research on animal-transported subsidies by integrating animal movement and ecosystem modelling. *Journal of Animal Ecology*, 86(5), 987–997. <https://doi.org/10.1111/1365-2656.12711>
- Ebert, D. A., & Bizzarro, J. J. (2007). Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environmental Biology of Fishes*, 80(2–3), 221–237. <https://doi.org/10.1007/s10641-007-9227-4>
- Espinoza, M., Munroe, S. E., Clarke, T. M., Fisk, A. T., & Wehrmann, I. S. (2015). Feeding ecology of common demersal elasmobranch species in the Pacific coast of Costa Rica inferred from stable isotope and stomach content analyses. *Journal of Experimental Marine Biology and Ecology*, 470, 12–25. <https://doi.org/10.1016/j.jembe.2015.04.021>
- Estalles, M. L., Perier, M. R., & Di Giacomio, E. E. (2016). Trophic ecology of the smallnose fanskate *Sympterygia bonapartii* in the San Matías Gulf, northern Patagonia, Argentina. *Ichthyological Research*, 63(2), 207–217. <https://doi.org/10.1007/s10228-015-0489-0>
- Every, S. L., Pethybridge, H. R., Fulton, C. J., Kyne, P. M., & Crook, D. A. (2017). Niche metrics suggest euryhaline and coastal elasmobranchs provide trophic connections among marine and freshwater biomes in northern Australia. *Marine Ecology Progress Series*, 565, 181–196. <https://doi.org/10.3354/meps11995>
- Fall, J., & Fiksen, Ø. (2020). No room for dessert: A mechanistic model of prey selection in gut-limited predatory fish. *Fish and Fisheries*, 21(1), 63–79. <https://doi.org/10.1111/faf.12415>
- Figueiredo, I., Moura, T., Bordalo-Machado, P., Neves, A., Rosa, C., & Gordo, L. S. (2007). Evidence for temporal changes in ray and skate populations in the Portuguese coast (1998–2003)—its implications in the ecosystem. *Aquatic Living Resources*, 20(1), 85–93. <https://doi.org/10.1051/alr:2007019>
- Fonseca, G., Hutchings, P., Vieira, D. C., & Gallucci, F. (2011). Meiobenthic community underneath the carcass of a stingray a snapshot after natural death. *Aquatic Biology*, 13(1), 27–33. <https://doi.org/10.3354/ab00347>
- Gallagher, A. J., Vianna, G. M., Papastamatiou, Y. P., Macdonald, C., Guttridge, T. L., & Hammerschlag, N. (2015). Biological effects, conservation potential, and research priorities of shark diving tourism. *Biological Conservation*, 184, 365–379. <https://doi.org/10.1016/j.biocon.2015.02.007>
- Gaspar, C., Chateau, O., & Galzin, R. (2008). Feeding sites frequentation by the pink whipray *Himantura fai* in Moorea (French Polynesia) as determined by acoustic telemetry. *Cybiurn*, 32(2), 153–164.
- Glaspie, C. N., & Seitz, R. D. (2017). Role of habitat and predators in maintaining functional diversity of estuarine bivalves. *Marine Ecology Progress Series*, 570, 113–125. <https://doi.org/10.3354/meps12103>
- Grant, J. (1983). The relative magnitude of biological and physical sediment reworking in an intertidal community. *Journal of Marine Research*, 41(4), 673–689. <https://doi.org/10.1357/002224083788520469>
- Gray, A. E., Mulligan, T. J., & Hannah, R. W. (1997). Food habits, occurrence, and population structure of the bat ray, *Myliobatis californica*, in Humboldt Bay, California. *Environmental Biology of Fishes*, 49(2), 227–238.
- Grubbs, R. D., Carlson, J. K., Romine, J. G., Curtis, T. H., McElroy, W. D., McCandless, C. T., ... Musick, J. A. (2016). Critical assessment and ramifications of a purported marine trophic cascade. *Scientific Reports*, 6, 1–12. <https://doi.org/10.1038/srep20970>
- Haas, A. R., Fedler, T., & Brooks, E. J. (2017). The contemporary economic value of elasmobranchs in The Bahamas: Reaping the rewards of 25 years of stewardship and conservation. *Biological Conservation*, 207, 55–63. <https://doi.org/10.1016/j.biocon.2017.01.007>
- Hara, K., Furumitsu, K., & Yamaguchi, A. (2018). Dietary habits of the polkadot skate *Dipturus chinensis* in the East China Sea. *Ichthyological Research*, 65(3), 363–373. <https://doi.org/10.1007/s10228-018-0622-y>
- Hazen, E. L., Jorgensen, S., Rykaczewski, R. R., Bograd, S. J., Foley, D. G., Jonsen, I. D., ... Block, B. A. (2013). Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change*, 3(3), 234–238. <https://doi.org/10.1038/NCLIMATE1686>
- Heithaus, M. R. (2004). Predator-prey interactions. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *Biology of sharks and their relatives* (pp. 487–521). Boca Raton, FL: CRC Press.
- Heithaus, M. R., Frid, A., Vaudou, J. J., Worm, B., & Wirsing, A. J. (2010). Unraveling the ecological importance of elasmobranchs. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *Sharks and their relatives II* (pp. 627–654). Boca Raton, FL: CRC Press.
- Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, 23(4), 202–210. <https://doi.org/10.1016/j.tree.2008.01.003>
- Heupel, M. R., Knip, D. M., Simpfendorfer, C. A., & Dulvy, N. K. (2014). Sizing up the ecological role of sharks as predators. *Marine Ecology Progress Series*, 495, 291–298. <https://doi.org/10.3354/meps10597>
- Higgs, N. D., Gates, A. R., & Jones, D. O. B. (2014). Fish food in the deep sea: Revisiting the role of large food-falls. *PLoS One*, 9(5), <https://doi.org/10.1371/journal.pone.0096016>
- Hill, C. (1992). Interactions between year classes in the benthic amphipod *Monoporeia affinis*: Effects on juvenile survival and growth. *Oecologia*, 91(2), 157–162. <https://doi.org/10.1007/BF00317778>
- Hines, A. H., Whitlatch, R. B., Thrush, S. F., Hewitt, J. E., Cummings, V. J., Dayton, P. K., & Legendre, P. (1997). Nonlinear foraging response of a large marine predator to benthic prey: Eagle ray pits and bivalves in a New Zealand sandflat. *Journal of Experimental Marine Biology and Ecology*, 216(1–2), 191–210. [https://doi.org/10.1016/S0022-0981\(97\)00096-8](https://doi.org/10.1016/S0022-0981(97)00096-8)
- Hoff, G. R. (2009). Skate *Bathyraja* spp. egg predation in the eastern Bering Sea. *Journal of Fish Biology*, 74(1), 250–269. <https://doi.org/10.1111/j.1095-8649.2008.02137.x>
- Hosegood, J., Humble, E., Ogden, R., de Bruyn, M., Creer, S., Stevens, G., ... Carvalho, G. (2018). Phylogenomics and species delimitation of mobulid rays reveals cryptic diversity and a new species of manta ray. *bioRxiv*, 458141. <https://doi.org/10.1101/458141>
- Howard, J. D., Mayou, T. V., & Heard, R. W. (1977). Biogenic sedimentary structures formed by rays. *Journal of Sedimentary Research*, 47(1), 339–346.
- Jacobsen, I. P., & Bennett, M. B. (2013). A Comparative Analysis of Feeding and Trophic Level Ecology in Stingrays (Rajiformes; Myliobatoidei) and Electric Rays (Rajiformes; Torpedinoidei). *PLoS ONE*, 8(8), e71348. <http://dx.doi.org/10.1371/journal.pone.0071348>
- Kadri, H., Marouani, S., Bradai, M. N., & Bouaïn, A. (2014). Food habits of the brown ray *Raja miraletus* (Chondrichthyes: Rajidae) from the Gulf of Gabès (Tunisia). *Marine Biology Research*, 10(4), 426–434. <https://doi.org/10.1080/17451000.2013.797583>
- Kadri, H., Saïdi, B., Marouani, S., Bradai, M. N., & Bouaïn, A. (2013). Food habits of the rough ray *Raja radula* (Chondrichthyes: Rajidae) from the Gulf of Gabès (central Mediterranean Sea). *Italian Journal of Zoology*, 80(1), 52–59. <https://doi.org/10.1080/11250003.2012.697925>
- Kajiura, S. M., Maccles, L. J., Meredith, T. L., Cocks, K. L., & Dirk, L. J. (2009). Commensal foraging between double-crested cormorants and a southern stingray. *The Wilson Journal of Ornithology*, 646–648. <https://doi.org/10.1676/08-122.1>
- Kanno, S., Schlaff, A. M., Heupel, M. R., & Simpfendorfer, C. A. (2019). Stationary video monitoring reveals habitat use of stingrays in mangroves. *Marine Ecology Progress Series*, 621, 155–168. <https://doi.org/10.3354/meps12977>

- Kemper, J. M., Bizzarro, J. J., & Ebert, D. A. (2017). Dietary variability in two common Alaskan skates (*Bathyrja interrupta* and *Raja rhina*). *Marine Biology*, 164(3), 52. <https://doi.org/10.1007/s00227-017-3078-0>
- Kiszka, J. J., Heithaus, M. R., & Quod, J. P. (2015). Stingrays as possible facilitators for foraging trevallies in a nearshore sandflat. *Marine Biodiversity*, 45(4), 625–626. <https://doi.org/10.1007/s12526-014-0304-6>
- Koen Alonso, M., Crespo, E. A., García, N. A., Pedraza, S. N., Mariotti, P. A., Berón Vera, B., & Mora, N. J. (2001). Food habits of *Dipturus chilensis* (Pisces: Rajidae) off Patagonia, Argentina. *ICES Journal of Marine Science*, 58(1), 288–297. <https://doi.org/10.1006/jmsc.2000.1010>
- Kogure, K., & Wada, M. (2005). Impacts of macrobenthic bioturbation in marine sediment on bacterial metabolic activity. *Microbes and Environments*, 20(4), 191–199. <https://doi.org/10.1264/jsmc.20.191>
- Last, P. R., White, W. T., de Carvalho, M. R., Séret, B., Stehmann, M. F. W., & Naylor, G. J. P. (Eds.) (2016). *Rays of the world*. Clayton South, VIC: CSIRO.
- Lauder, G. V., & Di Santo, V. (2015). Swimming mechanics and energetics of elasmobranch fishes. In R. E. Shadwick, A. P. Farrell, & C. Brauner (Eds.), *Physiology of elasmobranch fishes: Structure and interaction with environment*, Fish Physiology, (Vol. 34A, pp. 219–253). Amsterdam, The Netherlands: Elsevier Science.
- Laverock, B., Gilbert, J. A., Tait, K., Osborn, A. M., & Widdicombe, S. (2011). Bioturbation: Impact on the marine nitrogen cycle. *Biochemical Society Transactions*, 39(1), 315–320. <https://doi.org/10.1042/BST0390315>
- Lawrence, A. J., Budziak, A., Campbell, I., Cornish, A., Ender, I., Jeffries, B., ... Ward-Paige, C. A. (2016). *Responsible Shark & Ray Tourism: A guide to best practice*. Gland, Switzerland: WWF, and Rancho Santa Margarita, USA: Project AWARE and Dorset, UK: Manta Trust. Retrieved from https://www.projectaware.org/sites/default/files/2017-02/SharkandRays_BestPracticeGuide_2017_hires.pdf
- Lewis, A., & Newsome, D. (2003). Planning for stingray tourism at Hamelin Bay, Western Australia: The importance of stakeholder perspectives. *International Journal of Tourism Research*, 5(5), 331–346. <https://doi.org/10.1002/jtr.442>
- Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *The American Naturalist*, 153(6), 649–659. <https://doi.org/10.1086/303202>
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68(4), 619–640. <https://doi.org/10.1139/z90-092>
- Lipej, L., Mavrič, B., Paliska, D., & Capapé, C. (2013). Feeding habits of the pelagic stingray *Pteroplatytrygon violacea* (Chondrichthyes: Dasyatidae) in the Adriatic Sea. *Journal of the Marine Biological Association of the United Kingdom*, 93(2), 285–290. <https://doi.org/10.1017/S0025315412000197>
- Lloyd, J. (2017). *Chesapeake Bay's misguided war on the ray*. Hakai Magazine. Retrieved from <https://www.hakaimagazine.com>
- López-García, J., Navia, A. F., Mejía-Falla, P. A., & Rubio, E. A. (2012). Feeding habits and trophic ecology of *Dasyatis longa* (Elasmobranchii: Myliobatiformes): Sexual, temporal and ontogenetic effects. *Journal of Fish Biology*, 80(5), 1563–1579. <https://doi.org/10.1111/j.1095-8649.2012.03239.x>
- Lucifora, L. O., & García, V. B. (2004). Gastropod predation on egg cases of skates (Chondrichthyes, Rajidae) in the southwestern Atlantic: Quantification and life history implications. *Marine Biology*, 145(5), 917–922. <https://doi.org/10.1007/s00227-004-1377-8>
- Lucifora, L. O., Valero, J. L., Bremec, C. S., & Lasta, M. L. (2000). Feeding habits and prey selection by the skate *Dipturus chilensis* (Elasmobranchii: Rajidae) from the south-western Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 80(5), 953–954. <https://doi.org/10.1017/S002531540000299X>
- Mabragaña, E., & Giberto, D. A. (2007). Feeding ecology and abundance of two sympatric skates, the shortfin sand skate *Psammobatis normani* McEachran, and the smallthorn sand skate *P. rudis* Günther (Chondrichthyes, Rajidae), in the southwest Atlantic. *ICES Journal of Marine Science*, 64(5), 1017–1027.
- MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, 100(916), 603–609. <https://doi.org/10.1086/282454>
- Machado, P. B., Gordo, L. S., & Figueiredo, I. (2004). Skate and ray species composition in mainland Portugal from the commercial landings. *Aquatic Living Resources*, 17(2), 231–234. <https://doi.org/10.1051/alr:2004015>
- Madin, E. M. P., Dill, L. M., Ridlon, A. D., Heithaus, M. R., & Warner, R. R. (2016). Human activities change marine ecosystems by altering predation risk. *Global Change Biology*, 22, 44–60. <https://doi.org/10.1111/gcb.13083>
- Martins, A. P. B., Heupel, M. R., Chin, A., & Simpfendorfer, C. A. (2018). Batoid nurseries: Definition, use and importance. *Marine Ecology Progress Series*, 595, 253–267. <https://doi.org/10.3354/meps12545>
- Matern, S. A., Cech, J. J., & Hopkins, T. E. (2000). Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: Evidence for behavioral thermoregulation? *Environmental Biology of Fishes*, 58(2), 173–182.
- McGregor, F., Richardson, A. J., Armstrong, A. J., Armstrong, A. O., & Dudgeon, C. L. (2019). Rapid wound healing in a reef manta ray masks the extent of vessel strike. *PLoS One*, 14(12), e0225681. <https://doi.org/10.1371/journal.pone.0225681>
- McKinney, M. A., McMeans, B. C., Tomy, G. T., Rosenberg, B., Ferguson, S. H., Morris, A., ... Fisk, A. T. (2012). Trophic transfer of contaminants in a changing arctic marine food web: Cumberland Sound, Nunavut, Canada. *Environmental Science & Technology*, 46(18), 9914–9922. <https://doi.org/10.1021/es302761p>
- Meekan, M. G., Trevitt, L., Simpfendorfer, C. A., & White, W. (2016). The piggybacking stingray. *Coral Reefs*, 35(3), 1011. <https://doi.org/10.1007/s00338-016-1429-9>
- Meysman, F. J. R., Middelburg, J. J., & Heip, C. H. R. (2006). Bioturbation: A fresh look at Darwin's last idea. *Trends in Ecology & Evolution*, 21(12), 688–695. <https://doi.org/10.1016/j.tree.2006.08.002>
- Molina, J. M., & Cazorla, A. L. (2015). Biology of *Myliobatis goodei* (Springer, 1939), a widely distributed eagle ray, caught in northern Patagonia. *Journal of Sea Research*, 95, 106–114. <https://doi.org/10.1016/j.seares.2014.09.006>
- Moore, A. B. M., McCarthy, I. D., Carvalho, G. R., & Peirce, R. (2012). Species, sex, size and male maturity composition of previously unreported elasmobranch landings in Kuwait, Qatar and Abu Dhabi Emirate. *Journal of Fish Biology*, 80(5), 1619–1642. <https://doi.org/10.1111/j.1095-8649.2011.03210.x>
- Morato, T., Solà, E., Grós, M. P., & Menezes, G. (2003). Diets of thornback ray (*Raja clavata*) and tope shark (*Galeorhinus galeus*) in the bottom longline fishery of the Azores, northeastern Atlantic. *Fishery Bulletin*, 101(3), 590–602.
- Mulas, A., Bellodi, A., Cannas, R., Cau, A., Cuccu, D., Marongiu, M. F., ... Follesa, M. C. (2015). Diet and feeding behaviour of longnosed skate *Dipturus oxyrinchus*. *Journal of Fish Biology*, 86, 121–138. <https://doi.org/10.1111/jfb.12551>
- Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., & Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, 315(5820), 1846–1850. <https://doi.org/10.1126/science.1138657>
- Navarro, J., Coll, M., Preminger, M., & Palomera, I. (2013). Feeding ecology and trophic position of a Mediterranean endemic ray: Consistency between sexes, maturity stages and seasons. *Environmental Biology of Fishes*, 96(12), 1315–1328. <https://doi.org/10.1007/s10641-013-0109-7>
- Navarro-González, J. A., Bohórquez-Herrera, J., Navia, A. F., & Cruz-Escalona, V. H. (2012). Diet composition of batoids on the continental

- shelf off Nayarit and Sinaloa. *Mexico. Ciencias Marinas*, 38(2), 347–362. <https://doi.org/10.7773/cm.v38i2.1999>
- Navia, A. F., Cortés, E., & Mejía-Falla, P. A. (2010). Topological analysis of the ecological importance of elasmobranch fishes: A food web study on the Gulf of Tortugas. *Colombia. Ecological Modelling*, 221(24), 2918–2926. <https://doi.org/10.1016/j.ecolmodel.2010.09.006>
- Navia, A. F., Mejía-Falla, P. A., López-García, J., Giraldo, A., & Cruz-Escalona, V. H. (2016). How many trophic roles can elasmobranchs play in a marine tropical network? *Marine and Freshwater Research*, 68(7), 1342–1353. <https://doi.org/10.1071/MF16161>
- Neto, D. G., & Carvalho, L. N. (2011). Nuclear-follower foraging associations among Characiformes fishes and Potamotrygonidae rays in clean waters environments of Teles Pires and Xingu rivers basins. *Midwest Brazil. Biota Neotropica*, 11(4), 359–362. <https://doi.org/10.1590/S1676-06032011000400030>
- Newsome, D., Lewis, A., & Moncrieff, D. (2004). Impacts and risks associated with developing, but unsupervised, stingray tourism at Hamelin Bay, Western Australia. *International Journal of Tourism Research*, 6(5), 305–323. <https://doi.org/10.1002/jtr.491>
- Norman, J. R. (1939). Remoras or sucking-fishes. *Nature*, 143(3611), 52–55.
- O'Malley, M. P., Lee-Brooks, K., & Medd, H. B. (2013). The global economic impact of manta ray watching tourism. *PLoS One*, 8(5), e65051. <https://doi.org/10.1371/journal.pone.0065051>
- O'Shea, O. R., Kingsford, M. J., & Seymour, J. (2010). Tide-related periodicity of manta rays and sharks to cleaning stations on a coral reef. *Marine and Freshwater Research*, 61(1), 65–73. <https://doi.org/10.1071/MF08301>
- Oñate-González, E. C., Amezcua, F., Buszkiewicz, J., Castellanos-Cendales, A. L., & Amezcua-Linares, F. (2017). Trophic ecology of the blotched stingray, *Urotrygon chilensis* (Elasmobranchii: Myliobatiformes: Urotrygonidae), in three areas of the Mexican Pacific. *Acta Ichthyologica Et Piscatoria*, 47(2), 185–196. <https://doi.org/10.3750/AIEP/02099>
- Orlov, A. M. (1998). On feeding of mass species of deep-sea skates (*Bathyrhaja* spp., Rajidae) from the Pacific Waters. *Journal of Ichthyology*, 38(8), 635–644.
- O'Shea, O. R., Thums, M., van Keulen, M., Kempster, R. M., & Meekan, M. G. (2013). Dietary partitioning by five sympatric species of stingray (Dasyatidae) on coral reefs. *Journal of Fish Biology*, 82(6), 1805–1820. <https://doi.org/10.1111/jfb.12104>
- O'Shea, O. R., Thums, M., van Keulen, M., & Meekan, M. (2012). Bioturbation by stingrays at Ningaloo Reef, Western Australia. *Marine and Freshwater Research*, 63(3), 189–197. <https://doi.org/10.1071/MF11180>
- Papastamatiou, Y. P., Grubbs, R. D., Imhoff, J. L., Gulak, S. J., Carlson, J. K., & Burgess, G. H. (2015). A subtropical embayment serves as essential habitat for sub-adults and adults of the critically endangered small-tooth sawfish. *Global Ecology and Conservation*, 3, 764–775. <https://doi.org/10.1016/j.gecco.2015.03.003>
- Papastamatiou, Y. P., Watanabe, Y. Y., Bradley, D., Dee, L. E., Weng, K., Lowe, C. G., & Caselle, J. E. (2015). Drivers of daily routines in an ectothermic marine predator: Hunt warm, rest warmer? *PLoS One*, 10(6), e0127807. <https://doi.org/10.1371/journal.pone.0127807>
- Papastamatiou, Y. P., Wetherbee, B. M., Lowe, C. G., & Crow, G. L. (2006). Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: Evidence for resource partitioning and competitive exclusion. *Marine Ecology Progress Series*, 320, 239–251. <https://doi.org/10.3354/meps320239>
- Pardo, S. A., Burgess, K. B., Teixeira, D., & Bennett, M. B. (2015). Local-scale resource partitioning by stingrays on an intertidal flat. *Marine Ecology Progress Series*, 533, 205–218. <https://doi.org/10.3354/meps11358>
- Peacor, S. D., & Werner, E. E. (2000). Predator effects on an assemblage of consumers through induced changes in consumer foraging behavior. *Ecology*, 81(7), 1998–2010. [https://doi.org/10.1890/0012-9658\(2000\)081\[1998:PEOAAO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1998:PEOAAO]2.0.CO;2)
- Peel, L. R., Daly, R., Keating Daly, C. A., Stevens, G. M., Collin, S. P., & Meekan, M. G. (2019). Stable isotope analyses reveal unique trophic role of reef manta rays (*Mobula alfredi*) at a remote coral reef. *Royal Society Open Science*, 6(9), 190599. <https://doi.org/10.1098/rsos.190599>
- Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science*, 308(5730), 1912–1915. <https://doi.org/10.1126/science.1111322>
- Peterson, C. H., Ambrose, W. G. Jr, & Hunt, J. H. (1982). A field test of the swimming response of the bay scallop (*Argopecten irradians*) to changing biological factors. *Bulletin of Marine Science*, 32(4), 939–944.
- Peterson, C. H., Fodrie, F. J., Summerson, H. C., & Powers, S. P. (2001). Site-specific and density-dependent extinction of prey by schooling rays: Generation of a population sink in top-quality habitat for bay scallops. *Oecologia*, 129, 349–356. <https://doi.org/10.1007/s004420100742>
- Peterson, H., Summerson, H. C., Prescott, C., & Fegley, R. (1989). Timing, intensity and sources of autumn mortality of adult, bay scallops *Argopecten irradians concentricus* Say. *Journal of Experimental Marine Biology and Ecology*, 127, 121–140. [https://doi.org/10.1016/0022-0981\(89\)90179-2](https://doi.org/10.1016/0022-0981(89)90179-2)
- Pini-Fitzsimmons, J., Knott, N. A., & Brown, C. (2018). Effects of food provisioning on site use in the short-tail stingray *Bathytoshia brevicaudata*. *Marine Ecology Progress Series*, 600, 99–110. <https://doi.org/10.3354/meps12661>
- Platell, M. E., Potter, I. C., & Clarke, K. R. (1998). Resource partitioning by four species of elasmobranchs (Batoidea: Urolophidae) in coastal waters of temperate Australia. *Marine Biology*, 131(4), 719–734. <https://doi.org/10.1007/s002270050363>
- Poulakis, G. R., Urakawa, H., Stevens, P. W., Deangelo, J. A., Timmers, A. A., Grubbs, R. D., ... Olin, J. A. (2017). Sympatric elasmobranchs and fecal samples provide insight into the trophic ecology of the small-tooth sawfish. *Endangered Species Research*, 32, 491–506. <https://doi.org/10.3354/esr00824>
- Powers, S. P., & Peterson, C. H. (2000). Conditional density dependence: The flow trigger to expression of density-dependent emigration in bay scallops. *Limnology and Oceanography*, 45(3), 727–732. <https://doi.org/10.4319/lo.2000.45.3.0727>
- Pradervand, P., Mann, B. Q., & Bellis, M. F. (2007). Long-term trends in the competitive shore fishery along the KwaZulu-Natal coast, South Africa. *African Zoology*, 42(2), 216–236. <https://doi.org/10.1080/15627020.2007.11407399>
- Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86(2), 501–509. <https://doi.org/10.1890/04-0719>
- Proulx, S. R., Promislow, D. E., & Phillips, P. C. (2005). Network thinking in ecology and evolution. *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>
- Rastgoo, A. R., & Navarro, J. (2016). Trophic levels of teleost and elasmobranch species in the Persian Gulf and Oman Sea. *Journal of Applied Ichthyology*, 33(3), 403–408. <https://doi.org/10.1111/jai.13249>
- Rastgoo, A. R., Navarro, J., & Valinassab, T. (2018). Comparative diets of sympatric batoid elasmobranchs in the Gulf of Oman. *Aquatic Biology*, 27, 35–41. <https://doi.org/10.3354/ab00694>
- Razzaghi, M., Mashjoor, S., & Kamrani, E. (2017). Mean trophic level of coastal fisheries landings in the Persian Gulf (Hormuzgan Province), 2002–2011. *Chinese Journal of Oceanology and Limnology*, 35(3), 528–536. <https://doi.org/10.1007/s00343-017-5311-6>
- Reidenauer, J. A., & Thistle, D. (1981). Response of a soft-bottom harpacticoid community to stingray (*Dasyatis sabina*) disturbance. *Marine Biology*, 267, 261–267. <https://doi.org/10.1007/BF00397120>
- Ripple, W. J., & Beschta, R. L. (2006). Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park.

- Biological Conservation*, 133(4), 397–408. <https://doi.org/10.1016/j.biocon.2006.07.002>
- Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12(9), 982–998. <https://doi.org/10.1111/j.1461-0248.2009.01347.x>
- Ritter, E. K., & Brunnenschweiler, J. M. (2003). Do sharksuckers, *Echeneis naucrates*, induce jump behaviour in blacktip sharks, *Carcharhinus limbatus*? *Marine and Freshwater Behaviour and Physiology*, 36(2), 111–113. <https://doi.org/10.1080/1023624031000119584>
- Roff, G., Doropoulos, C., Rogers, A., Bozec, Y. M., Krueck, N. C., Aurellado, E., ... Mumby, P. J. (2016). The ecological role of sharks on coral reefs. *Trends in Ecology & Evolution*, 31(5), 395–407. <https://doi.org/10.1016/j.tree.2016.02.014>
- Rose, M. D., & Polis, G. A. (1998). The distribution and abundance of coyotes: The effects of allochthonous food subsidies from the sea. *Ecology*, 79(3), 998–1007. [https://doi.org/10.1890/0012-9658\(1998\)079\[0998:TDAOC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[0998:TDAOC]2.0.CO;2)
- Ruocco, N. L., & Lucifora, L. O. (2017). Ecological singularity of temperate mesopredatory myliobatoid rays (Chondrichthyes: Myliobatiformes). *Marine and Freshwater Research*, 68(6), 1098–1111. <https://doi.org/10.1071/MF15469>
- Ruocco, N. L., Lucifora, L. O., Díaz de Astarloa, J. M., & Menni, R. C. (2012). From coexistence to competitive exclusion: Can overfishing change the outcome of competition in skates (Chondrichthyes, Rajidae)? *Latin American Journal of Aquatic Research*, 40(1), 102–112. <https://doi.org/10.3856/vol40-issue1-fulltext-10>
- Saglam, H., Ak, O., Kutlu, S., & Aydin, İ. (2010). Diet and feeding strategy of the common stingray *Dasyatis pastinaca* (Linnaeus, 1758) on the Turkish coast of southeastern Black Sea. *Cahiers De Biologie Marine*, 51(1), 37–44.
- Saglam, H., & Bascinar, N. S. (2008). Feeding ecology of thornback ray (*Raja clavata* Linnaeus, 1758) on the Turkish coast of the south-eastern Black Sea. *Marine Biology Research*, 4(6), 451–457. <https://doi.org/10.1080/17451000802233393>
- Sampson, L., Galván-Magaña, F., De Silva-Dávila, R., Aguiñiga-García, S., & O'Sullivan, J. B. (2010). Diet and trophic position of the devil rays *Mobula thurstoni* and *Mobula japanica* as inferred from stable isotope analysis. *Journal of the Marine Biological Association of the United Kingdom*, 90(5), 969–976. <https://doi.org/10.1017/S0025315410000548>
- San Martín, M. J., Braccini, J. M., Tamini, L. L., Chiamonte, G. E., & Perez, J. E. (2007). Temporal and sexual effects in the feeding ecology of the marbled sand skate *Psammobatis bergi* Marini, 1932. *Marine Biology*, 151(2), 505–513. <https://doi.org/10.1007/s00227-006-0499-6>
- Sarkar, K., & Khajanchi, S. (2020). Impact of fear effect on the growth of prey in a predator-prey interaction model. *Ecological Complexity*, 42, 100826. <https://doi.org/10.1016/j.ecocom.2020.100826>
- Schlaff, A. M., Heupel, M. R., & Simpfendorfer, C. A. (2014). Influence of environmental factors on shark and ray movement, behaviour and habitat use: A review. *Reviews in Fish Biology and Fisheries*, 24(4), 1089–1103. <https://doi.org/10.1007/s11160-014-9364-8>
- Schmitz, O. J., Beckerman, A. P., & O'Brien, K. M. (1997). Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology*, 78(5), 1388–1399. [https://doi.org/10.1890/0012-9658\(1997\)078\[1388:BMTCEO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1388:BMTCEO]2.0.CO;2)
- Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, 185(4145), 27–39. <https://doi.org/10.1126/science.185.4145.27>
- Schwartz, F. J. (1977). Effects of the sharksucker, *Echeneis naucrates*, disk on scaled and scaleless fish and sea turtles. *ASB Bull*, 24, 84.
- Semeniuk, C. A. D., Bourgeon, S., Smith, S. L., & Rothley, K. D. (2009). Hematological differences between stingrays at tourist and non-visited sites suggest physiological costs of wildlife tourism. *Biological Conservation*, 142(8), 1818–1829. <https://doi.org/10.1016/j.biocon.2009.03.022>
- Semeniuk, C. A. D., & Dill, L. M. (2006). Anti-predator benefits of mixed-species groups of cowtail stingrays (*Pastinachus sephen*) and whiprays (*Himantura uarnak*) at rest. *Ethology*, 112(1), 33–43. <https://doi.org/10.1111/j.1439-0310.2006.01108.x>
- Semeniuk, C. A., & Rothley, K. D. (2008). Costs of group-living for a normally solitary forager: Effects of provisioning tourism on southern stingrays *Dasyatis americana*. *Marine Ecology Progress Series*, 357, 271–282. <https://doi.org/10.3354/meps07299>
- Semeniuk, C. A., Speers-Roesch, B., & Rothley, K. D. (2007). Using fatty-acid profile analysis as an ecologic indicator in the management of tourist impacts on marine wildlife: A case of stingray-feeding in the Caribbean. *Environmental Management*, 40(4), 665–677. <https://doi.org/10.1007/s00267-006-0321-8>
- Sha, A., Samanta, S., Martcheva, M., & Chattopadhyay, J. (2019). Backward bifurcation, oscillations and chaos in an eco-epidemiological model with fear effect. *Journal of Biological Dynamics*, 13(1), 301–327. <https://doi.org/10.1080/17513758.2019.1593525>
- Shackley, M. (1998). 'Stingray City'-managing the impact of underwater tourism in the Cayman Islands. *Journal of Sustainable Tourism*, 6(4), 328–338. <https://doi.org/10.1080/09669589808667320>
- Sherman, C. S., Heupel, M. R., Moore, S. K., Chin, A., & Simpfendorfer, C. A. (2020). When sharks are away, rays will play: Effects of top predator removal in coral reef ecosystems. *Marine Ecology Progress Series*, 641, 145–157. <https://doi.org/10.3354/meps13307>
- Sherman, K. M., Reidenauer, J. A., Thistle, D., & Meeter, D. (1983). Role of a natural disturbance in an assemblage of marine free-living nematodes. *Marine Ecology Progress Series*, 11(1), 23–30. <https://doi.org/10.3354/meps011023>
- Shibuya, A., Araújo, M. L. G., & Zuanon, J. A. S. (2009). Analysis of stomach contents of freshwater stingrays (Elasmobranchii, Potamotrygonidae) from the middle Negro River, Amazonas, Brazil. *Pan-American Journal of Aquatic Sciences*, 4(4), 466–475.
- Sih, A., & Christensen, B. (2001). Optimal diet theory: When does it work, and when and why does it fail? *Animal Behaviour*, 61(2), 379–390. <https://doi.org/10.1006/anbe.2000.1592>
- Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, 15(3), 278–289. <https://doi.org/10.1111/j.1461-0248.2011.01731.x>
- Silva, J. F., Ellis, J. R., & Catchpole, T. L. (2012). Species composition of skates (Rajidae) in commercial fisheries around the British Isles and their discarding patterns. *Journal of Fish Biology*, 80, 1678–1703. <https://doi.org/10.1111/j.1095-8649.2012.03247.x>
- Silva-Garay, L., Pacheco, A. S., & Vélez-Zuazo, X. (2018). First assessment of the diet composition and trophic level of an assemblage of poorly known chondrichthyans off the central coast of Peru. *Environmental Biology of Fishes*, 101(10), 1525–1536. <https://doi.org/10.1007/s10641-018-0797-0>
- Sims, D. W., Wearmouth, V. J., Southall, E. J., Hill, J. M., Moore, P., Rawlinson, K., ... Nash, J. P. (2006). Hunt warm, rest cool: Bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology*, 75(1), 176–190. <https://doi.org/10.1111/j.1365-2656.2005.01033.x>
- Smale, M. J., & Cowley, P. D. (1992). The feeding ecology of skates (Batoidea: Rajidae) off the Cape south coast, South Africa. *South African Journal of Marine Science*, 12(1), 823–834. <https://doi.org/10.2989/02577619209504744>
- Smith, C., & Griffiths, C. (1997). Shark and skate egg-cases cast up on two South African beaches and their rates of hatching success, or causes of death. *African Zoology*, 32(4), 112–117. <https://doi.org/10.1080/02541858.1997.11448441>
- Smith, J. W., & Merriner, J. V. (1982). Association of cobia, *Rachycentron canadum*, with cownose ray, *Rhinoptera bonasus*. *Estuaries*, 5(3), 240–242. <https://doi.org/10.2307/1351842>
- Snelson, F. F., Gruber, S. H., Murru, F. L., & Schmid, T. H. (1990). Southern stingray, *Dasyatis americana*: Host for a symbiotic cleaner wrasse. *Copeia*, 1990, 961–965. <https://doi.org/10.2307/1446479>

- Souza, A. T., Ilarri, M. I., & Valentim, L. P. (2007). A 'hitch-hiker octopus' on a southern stingray at Fernando de Noronha Archipelago, SW Atlantic. *Coral Reefs*, 26(2), 333. <https://doi.org/10.1007/s00338-007-0199-9>
- Stevens, J. D., Bonfil, R., Dulvy, N. K., & Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, 57(3), 476–494. <https://doi.org/10.1006/jmsc.2000.0724>
- Stewart, J. D., Rohner, C. A., Araujo, G., Avila, J., Fernando, D., Forsberg, K., ... Semmens, B. X. (2017). Trophic overlap in mobulid rays: Insights from stable isotope analysis. *Marine Ecology Progress Series*, 580, 131–151. <https://doi.org/10.3354/meps12304>
- Strand, S. (1988). Following behavior: Interspecific foraging associations among Gulf of California reef fishes. *Copeia*, 1988(2), 351–357. <https://doi.org/10.2307/1445875>
- Swain, D. P., Benoît, H. P., & Hammill, M. O. (2015). Spatial distribution of fishes in a Northwest Atlantic ecosystem in relation to risk of predation by a marine mammal. *Journal of Animal Ecology*, 84(5), 1286–1298. <https://doi.org/10.1111/1365-2656.12391>
- Szczepanski, J. A., & Bengtson, D. A. (2014). Quantitative food habits of the bullnose ray, *Myliobatis freminvillii*, in Delaware Bay. *Environmental Biology of Fishes*, 97, 981–997. <https://doi.org/10.1007/s10641-014-0282-3>
- Takeuchi, S., & Tamaki, A. (2014). Assessment of benthic disturbance associated with stingray foraging for ghost shrimp by aerial survey over an intertidal sand flat. *Continental Shelf Research*, 84, 139–157. <https://doi.org/10.1016/j.csr.2014.05.007>
- Thorburn, D. C., Gill, H., & Morgan, D. L. (2014). Predator and prey interactions of fishes of a tropical Western Australia river revealed by dietary and stable isotope analyses. *Journal of the Royal Society of Western Australia*, 97, 363–387.
- Thrush, S. F., Pridmore, R. D., Hewitt, J. E., & Cummings, V. J. (1991). Impact of ray feeding disturbances on sandflat macrobenthos: Do communities dominated by polychaetes or shellfish respond differently? *Marine Ecology Progress Series*, 69, 245–252.
- Thrush, S. F., Pridmore, R. D., Hewitt, J. E., & Cummings, V. J. (1994). The importance of predators on a sandflat: Densities and predator effects. *Marine Ecology Progress Series*, 107, 211–222.
- Tilley, A., López-Angarita, J., & Turner, J. R. (2013a). Diet reconstruction and resource partitioning of a Caribbean marine mesopredator using stable isotope Bayesian modelling. *PLoS One*, 8(11), e79560. <https://doi.org/10.1371/journal.pone.0079560>
- Tilley, A., López-Angarita, J., & Turner, J. R. (2013b). Effects of scale and habitat distribution on the movement of the southern stingray *Dasyatis americana* on a Caribbean atoll. *Marine Ecology Progress Series*, 482, 169–179. <https://doi.org/10.3354/meps10285>
- Topelko, K. N., & Dearden, P. (2005). The shark watching industry and its potential contribution to shark conservation. *Journal of Ecotourism*, 4(2), 108–128. <https://doi.org/10.1080/14724040409480343>
- Treloar, M. A., Laurie, J., Laurenson, B., & Stevens, J. D. (2007). Dietary comparisons of six skate species (Rajidae) in south-eastern Australian waters. *Environmental Biology of Fishes*, 80(2–3), 181–196. <https://doi.org/10.1007/s10641-007-9233-6>
- Valenzuela-Quinonez, F., Galván-Magaña, F., Ebert, D. A., & Aragón-Noriega, E. A. (2018). Feeding habits and trophic level of the shovel-nose guitarfish (*Pseudobatos productus*) in the upper Gulf of California. *Journal of the Marine Biological Association of the United Kingdom*, 98(7), 1783–1792. <https://doi.org/10.1017/S0025315417000832>
- van Hees, K., Pien, C., Ebert, D. A., Cailliet, G. M., & Smith, W. D. (2015). *Myliobatis californicus*. The IUCN Red List of Threatened Species: e.T39416A80677869. Retrieved from <https://www.iucnredlist.org/species/39416/80677869>
- VanBlaricom, G. R. (1982). Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. *Ecological Monographs*, 52(3), 283–305. <https://doi.org/10.2307/2937332>
- Varghese, S. P., Somvanshi, V. S., & Dalvi, R. S. (2014). Diet composition, feeding niche partitioning and trophic organisation of large pelagic predatory fishes in the eastern Arabian Sea. *Hydrobiologia*, 736(1), 99–114. <https://doi.org/10.1007/s10750-014-1895-4>
- Vaudo, J. J., & Heithaus, M. R. (2011). Dietary niche overlap in a near-shore elasmobranch mesopredator community. *Marine Ecology Progress Series*, 425, 247–260. <https://doi.org/10.3354/meps08988>
- Vaudo, J. J., & Heithaus, M. R. (2013). Microhabitat selection by marine mesoconsumers in a thermally heterogeneous habitat: Behavioral thermoregulation or avoiding predation risk? *PLoS One*, 8(4), e61907. <https://doi.org/10.1371/journal.pone.0061907>
- Vaudo, J. J., Wetherbee, B. M., Harvey, G. C. M., Harvey, J. C., Prebble, A. J. F., Corcoran, M. J., ... Shivji, M. S. (2018). Characterisation and monitoring of one of the world's most valuable ecotourism animals, the southern stingray at Stingray City, Grand Cayman. *Marine and Freshwater Research*, 69(1), 144–154. <https://doi.org/10.1071/MF17030>
- Vaughan, D. B., Grutter, A. S., Costello, M. J., & Hutson, K. S. (2017). Cleaner fishes and shrimp diversity and a re-evaluation of cleaning symbioses. *Fish and Fisheries*, 18(4), 698–716. <https://doi.org/10.1111/faf.12198>
- Villegas-Ríos, D., Réale, D., Freitas, C., Moland, E., & Olsen, E. M. (2018). Personalities influence spatial responses to environmental fluctuations in wild fish. *Journal of Animal Ecology*, 87(5), 1309–1319. <https://doi.org/10.1111/1365-2656.12872>
- Visser, I. (1999). Benthic foraging on stingrays by killer whales (*Orcinus orca*) in New Zealand waters. *Marine Mammal Science*, 15(1), 220–227. <https://doi.org/10.1111/j.1748-7692.1999.tb00793.x>
- Walker, P. A., & Heessen, H. J. L. (1996). Long-term changes in ray populations in the North Sea. *ICES Journal of Marine Science*, 53(6), 1085–1093. <https://doi.org/10.1006/jmsc.1996.0135>
- Ward, P., & Myers, R. A. (2005). Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology*, 86(4), 835–847. <https://doi.org/10.1890/03-0746>
- Ward-Paige, C. A. (2017). A global overview of shark sanctuary regulations and their impact on shark fisheries. *Marine Policy*, 82, 87–97. <https://doi.org/10.1016/j.marpol.2017.05.004>
- Woodland, R. J., Secor, D. H., & Wedge, M. E. (2011). Trophic resource overlap between small elasmobranchs and sympatric teleosts in Mid-Atlantic Bight nearshore habitats. *Estuaries and Coasts*, 34(2), 391–404. <https://doi.org/10.1007/s12237-010-9331-0>
- Yahel, G., Yahel, R., Katz, T., Lazar, B., Herut, B., & Tunnicliffe, V. (2008). Fish activity: A major mechanism for sediment resuspension and organic matter remineralization in coastal marine sediments. *Marine Ecology Progress Series*, 372, 195–209. <https://doi.org/10.3354/meps07688>
- Yahel, R., Yahel, G., & Genin, A. (2002). Daily cycles of suspended sand at coral reefs: A biological control. *Limnology and Oceanography*, 47(4), 1071–1083. <https://doi.org/10.4319/lo.2002.47.4.1071>
- Yamaguchi, A., Furumitsu, K., Tanaka, S., & Kume, G. (2012). Dietary habits of the fanray *Platyrrhina tangi* (Batoidea: Platyrrhinidae) in Ariake Bay, Japan. *Environmental Biology of Fishes*, 95, 147–154. <https://doi.org/10.1007/s10641-011-9792-4>
- Yamaguchi, A., Kawahara, I., & Ito, S. (2005). Occurrence, growth and food of longheaded eagle ray, *Aetobatus flagellum*, in Ariake Sound, Kyushu, Japan. *Environmental Biology of Fishes*, 74, 229–238. <https://doi.org/10.1007/s10641-005-0217-0>
- Yano, K., Stevens, J. D., & Compagno, L. J. V. (2007). Distribution, reproduction and feeding of the Greenland shark *Somniosus (Somniosus) microcephalus*, with notes on two other sleeper sharks, *Somniosus (Somniosus) pacificus* and *Somniosus (Somniosus) antarcticus*. *Journal of Fish Biology*, 70(2), 374–390. <https://doi.org/10.1111/j.1095-8649.2007.01308.x>
- Yemişken, E., Forero, M. G., Megalofonou, P., Eryilmaz, L., & Navarro, J. (2018). Feeding habits of three Batoids in the Levantine Sea (north-eastern Mediterranean Sea) based on stomach content and isotopic data. *Journal of the Marine Biological Association of the*

United Kingdom, 98(1), 89–96. <https://doi.org/10.1017/S002531541700073X>

Yick, B. J. L., Tracey, S. R., & White, R. W. G. (2011). Niche overlap and trophic resource partitioning of two sympatric batoids co-inhabiting an estuarine system in southeast Australia. *Journal of Applied Ichthyology*, 27, 1272–1277. <https://doi.org/10.1111/j.1439-0426.2011.01819.x>

How to cite this article: Flowers KI, Heithaus MR, Papastamatiou YP. Buried in the sand: Uncovering the ecological roles and importance of rays. *Fish Fish*. 2021;22:105–127. <https://doi.org/10.1111/faf.12508>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.