Review

Measuring the occurrence and strength of intraguild predation in modern food webs

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ABSTRACT

Intraguild predation (IGP) is a complex, multi-species interaction that simultaneously combines predation and competition among a minimum of three individuals - a predator ($IG_{predator}$) that kills and consumes prey (IG_{prey}) with which it competes for a common resource, resulting in a 'trophic loop'. Although ubiquitous, IGP occurrence and strength vary across functional groups, trophic levels and ecosystems. A form of omnivory, changes to IGP trophic loops can have non-linear consequences that shape individual-, population- and community-level processes. This review i) synthesizes current knowledge on the methods available to measure the occurrence and strength of IGP in food webs from qualitative observation to complex quantitative models and ii) uses a two-tier approach to quantify research effort since the seminal work of Polis et al. (1989), and highlights important areas for future IGP research. Modern technological advancements, including diverse chemical tracers, telemetry with integrated sensors, and simulation modelling provide novel methods to address IGP knowledge gaps and improve understanding of how food webs will respond to perturbations. At the individual level, chemical and morphological changes in response to IGP require further study, while population- and community-level analyses require a focus on the resilience of common resources and changes in guild structure, respectively. The application of novel methods to investigate IGP will result in an improved understanding of the underlying mechanisms responsible for ecosystem function.

Contents

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1. Introduction

Hierarchical animal interactions drive the structure of food webs and ultimately determine ecosystem stability and function. An understanding of species interactions within food webs allows one to predict the consequences of species depletion or loss from perturbations such as overexploitation, habitat loss and climate change (Pimm, 1980; Polis and Strong, 1996). Animal interactions have traditionally been studied by examining the inter-relationship between two species. This, however, ignores the fact that multi-species interactions can have complex, indirect effects within food webs. Intraguild predation (IGP) is a more holistic approach to study animal interactions. A form of omnivory, IGP is a multi-trophic interaction that forms a 'trophic loop' - a closed pathway of trophic links (Neutel et al., 2002). Intraguild predation simultaneously combines predation and competition among a minimum of three species; an intraguild predator (IG$_{predator}$) that kills and consumes an intraguild prey (IG$_{prey}$), with which it competes for a common resource (Polis et al., 1989).

The seminal theoretical IGP framework by Polis et al. (1989) identified two main descriptors involved in this multi-species interaction: symmetry and age structure. Symmetry is classified as either asymmetrical, with one clearly defined IG$_{predator}$ and IG$_{prey,}$ or, symmetrical whereby role reversal between IGP$_{consumers}$ (i.e. IG$_{predator}$ and IG$_{prey}$) occurs. Age structure may be unimportant or important, and when important, IGP occurs solely between individuals in a particular age class. Four main IGP classes are currently defined: i) asymmetrical age-structure unimportant, ii) asymmetrical age-structure important, iii) symmetrical age-structure unimportant and iv) symmetrical age-structure important (Fig. 1).

Intraguild predation is highly relevant in the modern era of ecosystem-based studies as the occurrence of trophic loops can shape individual-, population- and community-level processes (McCann et al., 1998). Intraguild predation interactions, for example, can determine the strength, direction and linearity of trophic cascades, developmental bottlenecks, and biomass availability across trophic levels (Holt and Polis, 1997). This review i) provides an overview of the methods available to measure the occurrence and strength of IGP within food webs from qualitative observation, to complex quantitative simulation models and ii) determines the overall research effort focused on IGP since Polis et al. (1989) from the individual to the community level to identify IGP knowledge gaps that require focused study.

2. Methods used to study the occurrence and strength of IGP

Confirmation of the presence of IGP within a food web requires verification of predation and consumption of an IG$_{prey}$ by an IG$_{predator}$, that the IGP$_{consumers}$ are sympatric (i.e. have overlapping niches and occupy the same environment at the same time) and compete for a common resource (Guzmán et al., 2016; Fonseca et al., 2017). Without sufficient evidence of consumption after a kill, a predator may merely exhibit an extreme form of interference competition whereby one predator reduces competition through killing, commonly termed 'interspecific killing' (Palomares and Caro, 1999). In a systematic review of literature that examined lethal interactions among apex vertebrae predators, 48% of the studies failed to mention consumption of a prey item by the predator (Lourenço et al., 2014). Verification of predation, consumption and competitive interactions is thus fundamental to accurately describe IGP within the context of a food web. This section explores existing methods to measure the occurrence and strength of IGP in the literature to date and provides novel approaches that may be used in future IGP studies. For a complete list of approaches discussed refer to Table 1.

2.1. Approaches for direct observation of IGP in real-time/near real-time

Historically, the existence of IGP among species was determined through direct observation of predation and consumption of IG$_{prey}$ by an IG$_{predator}$ (Polis and McCormick, 1986). Opportunistic direct observation of IGP is still reported in the modern literature, for example, Fallows et al. (2015) confirmed IGP by a Cape fur seal (*Arctocephalus pusillus*; IG$_{predator}$), on a juvenile blue shark (*Prionace glauca*; IG$_{prey}$), with videography and photography (Fig. 2A). Recording technologies, including photography (Gilman, 2016; Fig. 2B), videography (Oppenheim and
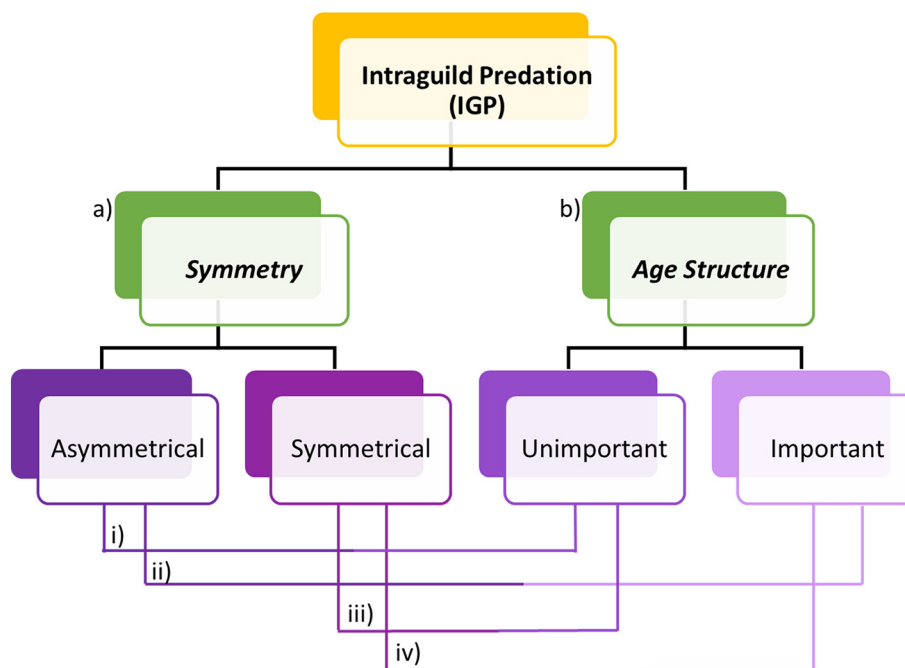
Fig. 1. Schematic of intraguild predation (IGP) and the two descriptors responsible for the different classes of IGP a) symmetry and b) age structure. Symmetry can either be asymmetrical with one clearly defined IG$_{predator}$ and one clearly defined IG$_{prey}$, or, symmetrical whereby role reversal between the IG$_{predator}$ and the IG$_{prey}$ is possible. Similarly, age structure can be unimportant for the interaction, or important whereby only certain age classes of species are involved in IGP interactions. The four resulting IGP classes are i) asymmetrical age-structure unimportant, ii) asymmetrical age-structure important, iii) symmetrical age-structure unimportant and iv) symmetrical age-structure important IGP.

Table 1
The diverse suite of methodological approaches available used to estimate the occurrence and strength of intraguild predation (IGP).

Categories	Methods		Author	Study Species
			Estimating Intraguild Predation	
			Example Studies	
Direct Observation	Opportunistic Observation		Fallows et al. (2015)	Cape fur seal (*Arctocephalus pusillus*) and blue shark (*Prionace glauca*)
	Recording	Photography	Gilman (2016)	Salticid (*Hyllus brevitarsus*) and large orb weaver (*Nephila senegalensis*)
		Videography	Oppenheim and Wahle (2013)	American Lobster (*Homarus americanus*)
		Audio Recordings	Bright (2008)	Feather pecking and non-feather pecking laying flocks
	Tracking	Radio-telemetry	Swanson et al. (2014)	African lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lycaon pictus*)
			Brandt and Lambin (2007)	Weasel (*Mustela nivalis*) and field vole (*Microtus agrestis*)
			Kozlowski et al. (2012)	Kit foxes (*Vulpes macrotis*) and coyotes (*Canis lactrans*)
		Satellite-telemetry	Srygley and Lorch (2016)	Mormon crickets (*Anabrus simplex*), digger wasps (*Palmodes laeviventris* and *P. Hesperus*)
			Ferguson et al. (1997)	Polar bears (*Ursus maritimus*)
		Stomach Temperature Pills (STP)	Heide-Jørgensen et al. (2014)	Narwhal (*Monodon monoceros*)
Retrospective Observation	Recording	Photography	Greenville et al. (2014)	Dingo (*C. dingo*), European red fox (*V. vulpes*) and feral cat (*Felis catus*)
		Videography	Kistner et al. (2017)	Asian citrus psyllid (*Diaphrina citri*), predators (e.g. lacewigs and hover flies) and Argentine ants (*Linepithema humile*)
	Tracking	Acoustic-telemetry	Baldwin et al. (2002)	Cuthroat Trout (*Oncorhynchus clarki utah*)
		Predation Detection Acoustic Tags (PDAT)	Schultz et al. (2017)	Chinook Salmon (*Oncorhynchus tshawytscha*) and Striped Bass (*Morone saxatilis*)
		Integrative biologging e.g. Accelerometry & video	Watanabe and Takahashi (2013)	Adélie penguins (*Pygoscelis adeliae*)
		e.g. Acoustic pH transmitter	Papastamatiou et al. (2007)	Blacktip reef sharks (*Carcharhinus melanopterus*)
		Faecal analysis	Walker et al. (2018)	Eastern chimpanzees (*Pan troglodytes schweinfurthii*)
		Stomach content analysis	Raab et al. (2012)	Anchovy (*Engraulis encrasicolus*), herring (*Clupea harengus*) and sprat (*Sprattus sprattus*)
			Tsunoda et al. (2017)	Golden jackal (*C. aureus*) and red fox (*V. Vulpes*)
Markers and/or Tracers	Biological Markers	Gel eletrophoresis	Wool et al. (1978)	Internal parasite (*Aphidius matricariae*) in Myzus persicae
		Enzyme-Linked Immunosorbent Assay (ELISA)	Ragsdale (1980)	Detection of *Nezara viridula* in predators
		Gas Chromatography Mass Spectrometry (GC-MS)	Knutsen and Vogt (1985)	Lobsters (*Homarus Gammarus* (L.)) and shrim (*Artemia sauna* (L.))
		DNA analysis	Wengert et al. (2013)	Fisher (*Martes pennanti*), domestic dog, mountain lion (*Puma concolor*), bobcat (*Lynx rufus*) and coyote (*Canis latrans*)
		Fatty acid analysis	Pethybridge et al. (2014)	White shark (*Carcharodon carcharias*)
	Chemical Tracers	Stable Isotope Analysis (SIA)	Rickers et al. (2006)	Wolf spider species (*Alopecosa cuneata* and *Pardosa palustris*), springtail (*Heteromurus nitidus*) and fruit fly (*Drosophila melanogaster*)
		Compound-Specific Stable Isotope Analysis (CSIA)	Chikaraishi et al. (2014)	200 free-roaming organisms, representing 39 species in coastal marine (a stony shore) and 38 species in terrestrial (a fruit farm) environments

Categories	Models	Author	Model Topic(s)
		Estimating Intraguild Predation	
		Example Studies	
Community Models	Traditional IGP	Grover (1995)	General Resource-Consumer Model identified criteria necessary for coexistence among IGP species.
		Löder et al. (2014)	Lotka – Volterra IGP Model of a microzooplankton community further highlighted scenarios for IGP species coexistence.
		Ruggieri and Schreiber (2005)	Incorporation of IGP into Schoener's Exploitative Competition Model resulted in the expanded range for alternative stable states. This study found an alternative stable state called 'contingent coexistence of the IGP species or displacement of the IGP' depending on initial species densities.
	Game Theoretical	Heithaus (2001)	IGP species coexistence occurred when dietary overlap was low, the shared resource had intermediate productivity and when an alternative resource (i.e. fourth species) was added for the IGpredator when resource productivity was high.
	Model comparisons	Takimoto et al. (2007)	3 vs. 4 trophic level model – alternative stable states were dependent on growth rates.
		Verdy and Amarasekare (2010)	Predicted biological conditions necessary for alternative stable states in communities with IGP.
Food Web Models	Niche	Williams and Martinez (2000)	Estimated the factors that contribute most to the complexity of a food web structure.
	Food web matrix	Arim and Marquet (2004)	Examined food web studies and determined IGP is ubiquitous in food webs.
Simulation	Multi-species	Andonegi et al.	OSMOSE used to assess stock populations of European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina*

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Table 1 (*continued*)

Categories	Models	Example Studies	
		Author	Model Topic(s)
Models	individual-based	(2013)	*pilchardus*)
	Minimum Realistic (MRM)	Ross-Gillespie (2016)	GADGET used to improve stock assessment of South African hake fishery comprised of shallow-water Cape hake (*Merluccius capensis*) and deep-water Cape hake (*M. paradoxus*)
	Dynamic System	Condie et al. (2014)	ATLANTIS determined lack of population recovery by eastern gemfish (*Rexea solandri*) was likely due to IGP interactions with arrow squid (*Nototodarus gouldi*)
	Whole Ecosystem	Kitchell et al. (2002)	EwE used to determine that predation by apex sharks on sharks (i.e. IGP) results in strong non-linear responses in food webs.

Estimating Intraguild Predation is the overall table heading.

Fig. 2. Examples of direct observation of intraguild predation. A) Opportunistic observation of a cape fur seal (*Arctocephalus pusillus*) consuming a blue shark (*Prionace glauca*) [from Fallows et al., 2015]. B) Photographic recording of intraguild predation between a salticid (*Hyllus brevitarsus*) and an orb weaver (*Nephila senegalensis*) [from Gilman (2016)]. C) Example of the use of radio telemetry on kissing bugs (*Triatoma gerstaeckeri*) [from Hamer et al., 2018]. D & E) Tracking equipment MK10-AL satellite and STP3 stomach temperature pill, respectively, deployed on leatherback turtles (*Dermochelys coriacea*) [from Casey et al., 2010].

Wahle, 2013) and audio recordings (Bright, 2008), can be used to document IGP interactions in real-time, and near real-time. Tracking technology, through radio (Hamer et al., 2018; Fig. 2C) and satellite telemetry (Casey et al., 2010; Fig. 2D), provide an alternative approach to document IGP through attachment of a tag to an animal that transmits location data in real-time (active radio telemetry) or near real-time (acoustic/ratio and satellite telemetry; Hussey et al., 2015). Radio-telemetry has documented IGP interactions among large terrestrial species such as cheetahs, wild dogs and lions (Swanson et al., 2014), medium-sized species such as weasels and voles (Brandt and Lambin, 2007), foxes and coyotes (Kozlowski et al., 2012), as well as smaller species including insects (e.g. Mormon crickets and digger wasps; Srygley and Lorch, 2016). It has also facilitated the study of IGP of hawks (e.g. sharp-shinned and Cooper's hawks; Roth and Lima, 2007) and owls (e.g. tawny and little owls; Michel et al., 2016), fish (e.g. pike; Cucherousset et al., 2009), crocodiles (Hutton, 1989) and revealed insights into IGP among invasive species (e.g. Jackson chameleon; Van Kleeck et al., 2018).

Passive satellite telemetry has enabled the study of IGP in logistically challenging environments, for example, to examine changes in the sheltering behaviour of female polar bears (*Ursus maritimus*) in response to cannibalism by males (Ferguson et al., 1997). A recent technological advancement, stomach temperature pills (STPs, Casey et al., 2010; Fig. 2E), provides evidence for predation events by homeothermic predators, such as narwhal (Heide-Jørgensen et al., 2014), in near real-time. Placed within the stomach, STPs monitor fluctuations in the gut temperature and relay data to a satellite transmitter attached to the predator, indicating the time and location of a suspected predation event (Casey et al., 2010; Heide-Jørgensen et al., 2014).

2.2. Methods for retrospective observation of IGP

2.2.1. Recording and tracking technology

Retrospective observation of IGP can be documented through passive photography and videography, whereby the device is set to document interactions at programmed recording intervals with data stored and evaluated after the event (Fedriani et al., 2000; Rich et al., 2017). For example, remote cameras were used to retrospectively assess the interactions between three sympatric species: the dingo (*Canis dingo*), European red fox (*Vulpes vulpes*) and feral cat (*Felis catus*; Greenville et al., 2014). Spatiotemporal interactions among the three species provided evidence of IGP by confirming high dietary overlap and consumption of the feral cat by the red fox (Greenville et al., 2014). Similarly, videography documented the efficiency of an ectoparasite, *Tamarixia radiata*, as a biological control for a population of Asian citrus psyllid, *Diaphrina citri*, a citrus pest that transmits *Candidatus Liberibacter spp.*, the causative agent of Citrus Greening disease (Halbert and Manjunath, 2004; Grafton-Cardwell et al., 2013). Video surveillance of species' activity patterns among citrus habitats examined the frequency and nature of *D. citri* interactions, including IGP, to determine the effectiveness of biological control for future integrated pest management approaches (Kistner et al., 2017; Fig. 3A).

Acoustic telemetry, a passive archival approach to monitor movements of fully aquatic species, remotely collects data on tagged fish when in range of fixed receivers or hydrophones. Data are subsequently downloaded periodically from recovered receivers (Hammerschlag et al., 2011; Tickler et al., 2019). Acoustic telemetry revealed that juvenile cutthroat trout, *Oncorhynchus clarki utah*, are most at risk of predation by adult conspecifics in early August when they are habitat-restricted due to hypoxia and higher lake temperatures (Baldwin et al., 2002). More recently, acoustic tags with a digestible fuse called predation detection acoustic tag (PDAT; Schultz et al., 2017; Fig. 3B) and predation tag (PT; Halfyard et al., 2017; Fig. 3C), have been developed to identify predation events post-consumption. Similar technology may also be effectively integrated into archival satellite tags widening the applicability of this approach (Meyer and Holland, 2012).

Integrative approaches that combine telemetry and archival biologgers with sensors (e.g. impedance tags, PDATs, accelerometers) and cameras can provide novel methods that reduce uncertainty in the identification and quantification of IGP events. For example, confirmation of predation has been validated through combined temperature and gastric pH data in an acoustic pH transmitter (Papastamatiou et al., 2007). Inserted into the stomachs of captive adult blacktip reef sharks, *Carcharhinus melanopterus*, the pH transmitters identified rapid increases in gastric pH associated with prey consumption (Papastamatiou et al., 2007). In Adélie penguins, *Pygoscelis adeliae*, the application of two accelerometers (placed on the head and body) coupled with a camera determined the type and number of foraging events (Watanabe and Takahashi, 2013), while animal-borne miniaturized mobile transceivers equipped with an accelerometer provided a framework for examining conspecific interactions among Greenland sharks (Barkley et al., 2020). These integrative approaches provide novel techniques with applications for studying IGP.

2.2.2. Approaches for dietary analysis of IGP

Traditionally diet composition of predatory species is retrospectively studied through faecal (Lockie, 1959) and stomach content analysis (SCA; Hyslop, 1980) as both methods are relatively cost-effective and can be non-invasive.

Faecal analysis. Faecal analysis is performed through the collection and examination of prey items in faecal matter (see Fig. 3D; Rodrigues et al., 2019). Once collected, prey is identified via hard boney parts that remain undigested, such as otoliths and dentaries from fish, insect exoskeletons, mammalian bones, fur and cranial structures (Trites and Joy, 2005). The use of faecal analysis in terrestrial studies has provided much insight into inter- and intra-specific behaviours of predators. The presence of undigested guard hairs in the faeces of the eastern chimpanzee (*Pan troglodytes schweinfurthii*), for example, revealed rare cannibalistic behaviour (Walker et al., 2018). Similarly, Gormezano and Rockwell (2013) examined the scat of polar bears, *U. maritimus*, and determined >6% of diet composition consisted of conspecifics. The authors also compared the current diet of polar bears with historical data collected 40 years ago and found an increase in prey such as snow geese, eggs and caribou. The study suggested that polar bears are opportunistic omnivores by incorporating novel resources into their diet and using IGP and cannibalism as adaptive foraging strategies in response to climate-induced shifts in available resources (Gormezano and Rockwell, 2013). Typically restricted to terrestrial studies, this method also has been used in the marine environment to study sperm whales (*Physeter macrocephalus*; Smith and Whitehead, 2000).

Stomach content analysis. Stomach content analysis (SCA) requires discerning gut contents through various stomach-emptying procedures including lethal dissection and non-lethal alternatives such as gastric lavage (Light et al., 1983), physical eversion of the stomach (Bush, 2003) and injection of an emetic to induce stomach eversion (Sims et al., 2000). Typically, SCA involves quantitative metrics such as count, volume and weight, similar to fecal analysis (Hynes, 1950; Hyslop, 1980; Dicken et al., 2017; Fig. 3E). For example, SCA examined the diet composition and possibility of IGP among three coexisting pelagic fish species of the North Sea (Raab et al., 2012). The three fish, European anchovy (*Engraulis encrasicolus*), juvenile herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) forage primarily on zooplankton, but can also incorporate fish into their diets (Huse and Toresen, 1996). Symmetrical IGP (see Fig. 1) is likely between the anchovy and sprat, as both species were found to consume fish (Raab et al., 2012). Alternatively, asymmetrical IGP (see Fig. 1) is expected between herring and other fish species as the herring diet contained no fish, suggesting they can act as IG$_{prey}$.
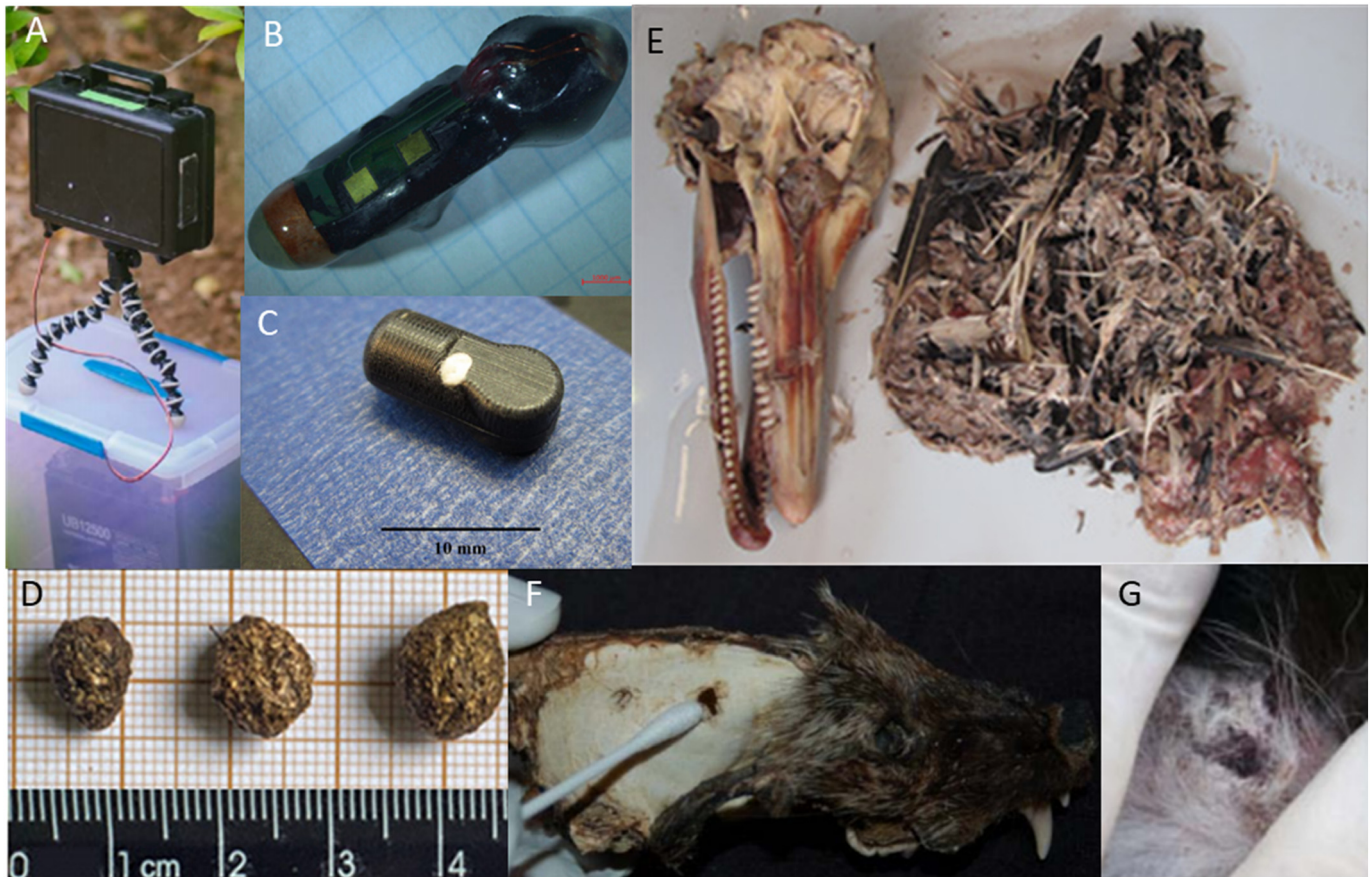
Fig. 3. Examples of methods used for the retrospective observation of intraguild predation. A) Recording technology, videograpy, used to study intraguild predation among Asian citrus psyllid (*Diaphrina citri*), predators (e.g. lacewigs and hover flies) and Argentine ants (*Linepithema humile*) [from Kistner et al., 2017]. B & C) Predator detection tags [from Schultz et al., 2017 and Halfyard et al., 2017, respectively]. D) Faecal pellets collected from the European hare (*Lepus europaeus*) for faecal analysis [from Rodrigues et al., 2019]. E) Stomach contents collected from a tiger shark (*Galeocerdo cuvier*) for stomach content analysis [from Dicken et al., 2017]. F & G) Collection of predator saliva and hair, respectively, from the carcass of a fisher (*Martes pennanti*) for DNA analysis [from Wengert et al., 2013 study].

Dietary composition studies have also studied IGP through SCA in terrestrial environments. Examination of gut contents provided a method for evaluating niche partitioning between a native canid, red fox (*V. vulpes*), and invasive golden jackal (*C. aureus*). Previous studies of newly invaded environments by the jackal (e.g. Hungary) demonstrated high dietary overlap between the golden jackal and red fox; the fox was also found in the diet of the jackal (Lanszki et al., 2006). For the coexistence of IGP$_{consumers}$, however, traditional IGP theory requires that IG$_{prey}$ (red fox) be superior at common resource acquisition (Polis et al., 1989; Holt and Polis, 1997). Stomach content analysis of carnivores in environments where the golden jackal had previously become established supported IGP theory, as the red fox continued to consume small rodents as a primary prey source while jackals (IG$_{predator}$) experienced substantial niche partitioning, shifting to a scavenger diet consisting of ungulate and domestic animal carcasses (Tsunoda et al., 2017).

2.3. Detection of IGP interactions via markers and/or tracers

Complementary techniques to SCA/faecal analysis include i) biological markers and ii) chemical tracers. Biological markers include identification of IGP species via enzymes, amino acids, DNA sequences, fatty acids and sterols, while chemical tracers include detection of elemental ratios such as carbon (^{12}C:^{13}C) and nitrogen (^{14}N:^{15}N), as well as additional elements such as mercury and sulphur. Each detection technique involves the identification of specific tracers from IGP species, however, there are fundamental differences between methods.

Integrated stomach/faecal and tracer approaches improve the resolution of IGP quantification through species-level identification of prey, providing greater confidence in results (Jarman et al., 2004).

2.3.1. Methods used to detect IGP with biological markers

Early predation studies (the late 1970s to early 1990s) on invertebrates used gel electrophoresis (Wool et al., 1978; Castañera et al., 1983), enzyme-linked immunosorbent assays (ELISA; Ragsdale, 1980) and gas chromatography–mass spectrometry (GC–MS; Knutsen and Vogt, 1985) for quantitative estimation of prey item consumption. While gel electrophoresis is a simple and affordable method used to sort prey enzymes and proteins by length, the test has limited sensitivity and is therefore incapable of identifying specific prey items from closely related species. Alternatively, ELISAs are highly sensitive as they immobilize antigens for identification of prey items through binding of specific prey monoclonal antibodies; however, generating prey-specific antibodies is time-consuming and therefore ELISAs are often used for identification of a single prey item rather than entire predatory diets (Traugott et al., 2013). Studies using GC–MS identify prey through prey chemicals found in predators, with prey detection rates and the accuracy of this method variable as target chemicals of prey (e.g. defensive chemicals) can be broken down or remain unmetabolized in the predator and therefore undetectable (Aebi et al., 2011). Despite the limitations, these methods are occasionally still used (Symondson, 2002; Aebi et al., 2011; Hagler et al., 2020). Technological advancements, however, have improved the accuracy and resolution of dietary analyses and

more advanced approaches, including DNA analysis, are now commonly used in IGP studies.

Diagnostic PCR used to detect DNA sequences. Application of DNA analysis to examine multi-species interactions of suspected IG$_{predators}$ using gut contents or faecal matter is a promising tool for future IGP studies. DNA analyses can be grouped into two different techniques; barcoding approaches and diagnostic polymerase chain reaction (PCR; Traugott et al., 2013). The first approach compares DNA sequences from prey to a barcode database of previously identified species (e.g. GenBank; Barnett et al., 2010). DNA analysis can be more targeted, however, if prior knowledge of consumer diet exists through group-specific PCR primers (Valentini et al., 2009). Diagnostic PCR involves the search for a specific species ('singleplex PCR') or several prey taxa simultaneously ('multiplex PCR') using PCR amplification of group-specific primers or species-specific targets (Tollit et al., 2009; Traugott et al., 2013). A study by Gagnon et al. (2011) successfully detected IGP among four closely related coccinellid species using PCR gut content analysis. Moreover, the study raised concern over variability in the detection of prey DNA post-feeding due to species-specific differences in rates of decay and variability among the size of prey items. This led to the development of an index of exponential decay approach (DS$_{50}$). Initial IGP among two coccinellid pairs (*Harmonia axyridis-Coleomegilla maculata* and *Coccinella septempunctata-H. axyridis*) identified significant differences in IGP occurrence (17.9% and 8.6%, respectively), yet DS$_{50}$ correction determined similar IGP occurrence between the pairs (scores of 0.07 and 0.08, respectively; Gagnon et al., 2011).

Other sources of DNA, such as saliva, blood, and hair, can also be used to identify IGP events. For example, amplified DNA from the saliva and hair of IG$_{predators}$ were collected from carcasses of fishers (*Martes pennant*; see Fig. 3F & G), a small endangered mammal native to North America, and primers specific to the DNA sequences of four suspected IG$_{predators}$ were used to confirm predation by the domestic dog, mountain lion (*Puma concolor*), bobcat (*Lynx rufus*) and coyote (*C. latrans*). Also, fisher skulls were examined for injuries sustained before death to identify which IG$_{predator}$ was involved. This integrated approach allowed the preferential selection of IG$_{prey}$ by IG$_{predators}$ to be examined; large IG$_{predators}$ (e.g. Mountain lion) foraged primarily on large male fishers, while smaller IG$_{predators}$ (e.g. bobcat) preferred small female fishers (Wengert et al., 2013).

Fatty acid analysis for IGP identification via fatty acid signatures. Fatty acids (FA) can also be used to investigate IGP (Iverson et al., 1997). Fatty acid profiles work on the premise that the average FA composition of prey eaten by a consumer experiences minimal change upon assimilation and is reflected in predator tissues (Iverson et al., 1995; Kirsch et al., 1998, 2000). The distinction of prey items within a consumer's diet is possible as some primary producers (e.g. plants, bacteria, fungi, algae) can synthesize unique FAs (e.g. γ-linolenic acid by protozoa; Lechevalier and Lechevalier, 1988). Consequently, FAs can differentiate prey items by taxa (e.g. mammals, birds and insects), species (e.g. 18:3ω3 is specific to macroalgae species), biome (e.g. terrestrial vs. aquatic), geographic range (e.g. latitude and temperature) and phylogeny (Colombo et al., 2016; Meyer et al., 2019). Pethybridge et al. (2014) observed differences in the FA profiles of the liver and muscle tissue in white sharks, *Carcharodon carcharias*, suggesting turnover rates or consumer ontogenetic diet shifts were responsible for the discrepancy between tissues. Although it was not the focus of the study, similarities in FA profiles between white sharks and suspected IG$_{prey}$ (e.g. marine mammals) could be used to indicate the presence of IGP in future studies.

2.3.2. Methods used to detect chemical markers and/or tracers

Bulk stable isotope analysis (SIA-Bulk) used to estimate IGP via elemental ratios. In the context of IGP, isotopic ratios of animal tissues act as the building blocks to determine the association between IG$_{predator}$ and IG$_{prey}$ (Peterson and Fry, 1987) through quantification of proportional IG$_{prey}$ isotopic contributions to the overall isotopic diet composition of an IG$_{predator}$ ("you are what you eat"; DeNiro and Epstein, 1981). Stable isotopes of carbon (^{12}C:^{13}C; $\delta^{13}C$; Inger and Bearhop, 2008), nitrogen (^{14}N:^{15}N; $\delta^{15}N$; Martínez del Rio et al., 2009), sulphur (^{32}S:^{34}S; $\delta^{34}S$; Goodenough, 2014) and mercury (Lourenço et al., 2011), among others, can be used to investigate the occurrence and strength of IGP. Establishing predator-prey interactions using bulk stable isotope analysis (SIA) is contingent on knowledge of tissue turnover rates and fractionation (the expected enrichment between predator and prey; Inger and Bearhop, 2008). Identification of specific prey species within a consumer diet may be difficult, however, (e.g. Hobson, 1993) as each prey item must be isotopically distinct (Harrigan et al., 1989; Doucett et al., 1996; Phillips et al., 2005). Modern mixing models, for example, SIAR and MixSIAR (Parnell et al., 2010; Stock et al., 2018), apply a Bayesian approach to SIA, incorporating species-specific isotopic values (i.e. distinct prey groups, IG$_{predator}$ and IG$_{prey}$) while accounting for variation in model parameters such as fractionation (Bond and Diamond, 2011), ultimately determining the relative contribution of IG$_{prey}$ items to total predator diet and inferring the strength of IGP (Rickers et al., 2006; Yurkowski et al., 2017).

An effective method to indirectly identify IGP, SIA monitored shifts in species interactions among two wolf spider species *Alopecosa cuneata* (IG$_{predator}$) and *Pardosa palustris* (IG$_{prey}$), a common resource (*Heteromurus nitidus*) and an alternative resource (*Drosophila melanogaster*; Rickers et al., 2006). Niche overlap between *A. cuneata* and the smaller *P. palustris* provides an ideal environment for asymmetrical age-structure important IGP (see Fig. 1). To ensure accurate interpretation of IG$_{predator}$ dietary switches, a marked difference in the $\delta^{13}C$ values between the alternative resource and IG$_{prey}$ tissues were established via ^{13}C enrichment of *D. melanogaster* before the study. Consumption of enriched *D. melanogaster* would, therefore, result in inflated $\delta^{13}C$ values of IG$_{predator}$ when consuming more of the alternate resource (Rickers et al., 2006). The occurrence of IGP was confirmed through a marked decrease in $\delta^{13}C$ values observed in IG$_{predator}$ tissue (Rickers et al., 2006).

Compound-specific stable isotope analysis (CSIA) to identify elemental ratios in specific amino acids/other biological markers. Compound-specific stable isotope analysis (CSIA) of select molecules, often amino acids and fatty acids, is assumed to address disadvantages in bulk SIA, for example, variability in baselines and among trophic discrimination factors (Blanke et al., 2017) through analyzing 'source' and 'trophic' molecules within a single tissue (McClelland and Montoya, 2002; Chikaraishi and Naraoka, 2003). Source amino acids (e.g. phenylalanine) have $\delta^{15}N$ signatures that are conserved across trophic levels and therefore act as a baseline, while trophic amino acids (e.g. glutamic acid) experience enrichment with each trophic level (Chikaraishi et al., 2009). Through improved precision of trophic position estimates and enhanced resolution of trophic interactions using CSIA of amino acids, Chikaraishi et al. (2014) were able to resolve the trophic structure of complex marine and terrestrial food webs, ultimately providing additional support for the prevalence of omnivory, including IGP, among food webs.

2.4. IGP modelling approaches

A hierarchy exists in a food web with individual-, population- and community-level processes interacting to form a complex network. An understanding of these multi-species, multi-level interactions is required before a more complete understanding of the structure and function of a food web is possible (Beckner, 1974). Since the acknowledgement of IGP in food webs by Polis et al. (1989), the study of multi-species interactions has followed a step-wise progression; early IGP calculations were first incorporated into existing, commonly used equations for individual species competition and predation (e.g.

Schoener's exploitative competition model; Schoener, 1976). Subsequent community models, or simple one-dimensional IGP models, accounted for additional food web complexity by incorporating factors such as foraging strategy and trophic level (Rosenheim and Corbett, 2003). Further complexity was incorporated through IGP model comparisons and by including the relative strength of species interactions, resulting in two-dimensional food web matrices (Arim and Marquet, 2004). Following the incorporation of additional variables and spatiotemporal parameters, three-dimensional ecosystem-based models were formed (e.g. Ecopath with Ecosim; Pauly and Christensen, 1995; Pauly et al., 1998). A holistic approach is necessary for the development of ecosystem-based management as system-wide conservation strategies have become a growing concern. This section is not a systematic review of all species interaction models that account for IGP, but rather provides a broad overview of the development and application of IGP modelling approaches to date.

2.4.1. Community models

Common mechanistic models to estimate the effects of IGP. To quantify the impacts of IGP at a population and community level, Holt and Polis (1997) incorporated IGP interactions into three commonly used mechanistic models: i) a general resource-consumer model, ii) the Lotka-Volterra model for a food chain and iii) the exploitative competition model of Schoener (1976). A mechanistic model of IGP examines: individual growth rate functions for the $IG_{predator}$, IG_{prey} and the common resource (P, N and R, respectively), functional responses of competing organisms [e.g. $\alpha(R, N, P)N$ is the $IG_{predator}$ response to IG_{prey}], a term for reproduction (e.g. b) and a term for the rate of mortality (e.g. m; Holt and Polis, 1997). Holt and Polis (1997) incorporated IGP into mechanistic models through the addition of terms such as, β, which represents the energetic benefit received by the $IG_{predator}$ from IG_{prey} consumption, and a recruitment term for the common resource [e.g. $R\phi(R)$; Holt and Polis, 1997]. Traditional IGP models are assumed to be asymmetrical, (Fig. 1) and exist as IGP 'community modules', a closed system whereby only the IGP species are interacting (Holt, 1997; Holt and Polis, 1997). One-dimensional models, therefore, provide the theoretical framework necessary to monitor changes in population dynamics in response to IGP and allow the possibility for non-linear functional responses (i.e. the feeding rate of a predator as a function of prey abundance; Holling, 1959; Skalski and Gilliam, 2001).

The addition of IGP into the resource-consumer model identified criteria necessary for coexistence among IGP species: i) superior exploitation of the common resource by the IG_{prey} following the R^* rule: $R^*_N < R^* < R^*_P$, where R is the growth rate of the IG_{prey}, resource and $IG_{predator}$, respectively (Tilman, 1990; Holt et al., 1994), ii) an immediate energetic gain by the $IG_{predator}$ from IG_{prey} consumption, and iii) an intermediate level of common resource productivity in environments with a productivity gradient (Holt and Polis, 1997; Grover, 1995). The addition of IGP into the resource-consumer model demonstrated that while the opportunity for stable coexistence of IGP species exists, under the criteria listed, the possibility for all criteria to be met at once is rare (Polis and Holt, 1992). The incorporation of IGP into the Lotka-Volterra food chain model required several assumptions: the common resource had a logistic growth rate in the absence of the $IG_{predator}$ and IG_{prey}, the growth rate of the $IGP_{consumers}$ were proportional to the rate of prey consumption (i.e. $IG_{predator}$ and IG_{prey} foraging rates were proportional to prey density), and the $IGP_{consumers}$ exhibited linear functional responses (Holt and Polis, 1997). The Lotka-Volterra IGP model resulted in five possible equilibria: i) all species with a density of zero, ii) the dominance of the common resource while the $IGP_{consumers}$ have a density of zero, iii) coexistence of the IGP species, and two possible alternative stable states. Alternative stable states exist whereby the system can experience different configurations dependent on initial parameters found within the model community (e.g. species densities; Beisner et al., 2003). The alternative stable

equilibria were iv) the $IG_{predator}$ and common resource coexist while the IG_{prey} is absent, or v) the IG_{prey} and common resource coexist while the $IG_{predator}$ density is zero. The model ultimately demonstrated that the long-term coexistence of IGP species may not be possible, despite mutual invasibility, due to unstable community dynamics driving species to low abundances (Holt and Huxel, 2007). The possibility for stable coexistence of species within an IGP module is therefore predicted by the Lotka-Volterra IGP model to be minimal (Holt and Polis, 1997). Altering Schoener's exploitative competition model (Schoener, 1976) to include IGP resulted in hyperbolic isoclines for the $IGP_{consumer}$ growth rates that expanded the range for alternative stable states, IGP species coexistence and reversal of competitive dominance between $IGP_{consumers}$. Furthermore, Ruggieri and Schreiber (2005), determined that there was an additional alternative stable state within the IGP community, that is, the contingent coexistence of the IGP species or displacement of the IG_{prey} depending on initial species densities. This alternative stable state, therefore, allowed for $IGP_{consumer}$ coexistence such that IG_{prey} density was not sufficiently reduced. A perturbation resulting in the loss of IG_{prey} abundance, however, resulted in the permanent exclusion of the IG_{prey} by the $IG_{predator}$ from the system (Ruggieri and Schreiber, 2005).

Results from empirical studies in support of theoretical IGP model predictions vary (Rosenheim et al., 1995; Mylius et al., 2001; Janssen et al., 2007) with most experimental evidence found in laboratory microcosm and parasitoid communities (Morin and Lawler, 1996; Amarasekare, 2000; Arim and Marquet, 2004). Morin (1999), for example, examined the influence of bacterial concentrations (common resource) on the density of ciliates in a freshwater microbial food web. The relationship between *Blepharisma americanum* ($IG_{predator}$), and *Colpidium striatum* (IG_{prey}) in a laboratory microcosm supported traditional IGP theory predictions; the $IG_{predator}$ was excluded at low bacterial concentrations and coexistence of IGP species occurred at higher common resource concentrations (Morin, 1999). Other laboratory experiments have confounding results at low common resource concentrations whereby IG_{prey} is excluded or there is no change in population density (Lawler and Morin, 1993; Janssen et al., 2006).

Although theoretical IGP models predict competitive exclusion or instability among IGP species, coexistence is commonly found in food webs (Brodeur and Rosenheim, 2000; Mylius et al., 2001; Arim and Marquet, 2004). The discrepancy between theory and observation may be a result of external factors in the food web that stabilize IGP species interactions and allow for coexistence; an interaction that IGP theoretical models would otherwise predict to result in IGP species extinctions (Wootton, 2017). Traditional theoretical models may, therefore, be limiting the possibility of species coexistence through assumptions such as the requirement for equilibrium dynamics, limiting species numbers to focused community modules (i.e. three or four species; Holt, 1997) and ignoring external factors such as environmental habitat structure (Janssen et al., 2007). A meta-analysis of IGP studies investigating the effect of habitat structure on IGP species indicated that complex habitats facilitate coexistence of IGP species (Janssen et al., 2007). The incorporation of additional species interactions, such as commensalism, into the Lotka-Volterra IGP model of a microzooplankton community further highlighted scenarios for IGP species coexistence (Löder et al., 2014). Holt and Huxel (2007) found the presence of a fourth species, an alternative prey source, within a community may provide increased opportunity for the coexistence of IGP species. Similarly, integration of a fourth species, thus an additional trophic link, into the Lotka-Volterra IGP model by Hall (2011), demonstrated that a specialized natural enemy can stabilize an IGP community and allow species coexistence regardless of the efficiency of the IG_{prey} at common resource acquisition. Through the preferential attack of a predator on the $IG_{predator}$, the stable presence of all IGP species was possible, even when the specialist predator was superior at competition for the common resource (Hall, 2011).

Game Theoretical Model Predicted Species Distributions Under IGP. The IGP game-theoretical model of habitat use predicts species distributions in the presence of asymmetrical IGP (Fig. 1) based on 5 factors: efficiency of resource exploitation, habitat complexity, dietary overlap, resource productivity and the availability of an additional resource (Heithaus, 2001). Through the incorporation of flexibility in species distributions, Heithaus (2001) determined IGP species coexistence occurred when dietary overlap was low and the shared resource had intermediate productivity. Additionally, coexistence of IGP$_{consumers}$ was possible in habitats with high resource productivity through the addition of an alternative resource, a fourth species, for consumption by the IG$_{predator}$. The game-theoretical IGP model provides novel insights into the indirect influence of alternative prey resources for the IG$_{predator}$ on community structure, and the spatial distribution of IG$_{prey}$ in response to i) habitat safety, ii) dietary overlap and iii) the balance between resource availability and predation risk (Heithaus, 2001).

Identifying conditions necessary for alternative stable states. The progression of IGP modelling continued through the comparison of model results from communities with different species compositions (Verdy and Amarasekare, 2010). For example, changes to common resource availability and productivity can alter community outcomes depending on the growth rate trajectories (i.e. logistic vs. exponential growth rates) and functional responses (i.e. Type I or II; Holling, 1959) of species within a community (Takimoto et al., 2007). Through comparing a tritrophic IGP model with one IGP species at each of the three trophic levels, to a model with four trophic levels through the addition of prey for the common resource, Takimoto et al. (2007) demonstrated that the possibility for alternative stable states was similar for each model, with results depending on the growth rates of the species within the system. Species growth rates were controlled by two main drivers: i) the identity of the IGP$_{consumer}$ with the competitive advantage for common resource exploitation, and ii) the efficiency of energy transfer from the common resource to the IG$_{predator}$ measured via body size (Takimoto et al., 2007).

Empirical studies have often failed to identify alternative stable states and therefore the frequency of this phenomenon was unknown in natural environments. Verdy and Amarasekare (2010) developed a model to predict the biological conditions necessary for the presence of alternative stable states in communities with IGP by examining community functional responses that were linear vs. non-linear (i.e. Type I or Type II, respectively; Holling, 1959) under two common resource growth rate trajectories, logistic vs. chemostatic (i.e. a constant environment with a growth rate of zero, $r = 0$). Model results highlighted three alternative stable state scenarios. Scenario i) the stable presence of an IGP$_{consumer}$; this scenario required the common resource exhibit logistic or chemostatic growth and the IGP$_{consumers}$ have linear or non-linear functional responses. Scenario ii) the coexistence of IGP$_{consumers}$ or dominance by the IG$_{predator}$; scenario ii required the common resource have a chemostatic growth rate and the IGP$_{consumers}$ have linear or non-linear functional responses. Scenario iii) the coexistence of IGP species or competitive dominance by the IG$_{prey}$; the last alternative stable state required the common resource exhibit logistic growth and the IGP$_{consumers}$ have non-linear functional responses (Verdy and Amarasekare, 2010). In a system with IGP interactions producing alternative stable states, the community can shift between scenarios in response to perturbation, thus impacting community diversity and ecosystem stability that result in changes to the structure and dynamics of entire ecosystems (Verdy and Amarasekare, 2010). Models with the ability to predict community composition based on IGP species growth rate dynamics and functional responses may, therefore, become an integral tool necessary for conservation efforts and ecosystem-based management strategies in the future.

2.4.2. Food web models

Early mathematical approaches failed to provide a mechanistic explanation for the full complexity of food webs. The 'niche model', for example, examined the strength of species interactions and estimated the factors (e.g. looping, omnivory, IGP) that contributed most to the complexity of food web structure (Williams and Martinez, 2000). This approach, based on an earlier 'cascade model' (Cohen et al., 1990), accounted for trophic similarity, length and number of food-chains in food webs by employing connectance (i.e. the proportion of links or species interactions observed) and species number as empirical parameters.

The incidence of IGP in food webs was first quantified using data from previously published food web studies (Arim and Marquet, 2004). Unlike earlier studies that assumed omnivory and IGP were destabilizing and rare in food webs (Pimm and Lawton, 1978; Pimm, 1982), this two-dimensional model quantitatively established that IGP is common in food webs. Species were categorized into 'trophic groups', a biologically meaningful way of classifying species using both functional role (Cohen et al., 1990) and foraging type (Arim and Marquet, 2004). The relative contribution of trophic groups to the overall prevalence of IGP in food webs was developed from food web matrices and analyzed using a null model approach. IGP existed in more than half (58–87%) of all food webs analyzed, with each trophic group participating in IGP at a different frequency (Arim and Marquet, 2004).

2.4.3. Simulation models

Simulation models expand on previous one- and two-dimensional IGP models, providing a method to predict how an ecosystem may change in response to proposed management strategies or perturbations (e.g. global climate change; Fulton, 2010). An outline for the existing multi-species model categories was originally presented by Hollowed et al. (2000) and updated by Plagányi (2007). The categories include species number (single- vs. multi-species; Hollowed et al., 2000), trophic level (lower vs. higher trophic level; Daewel et al., 2014), model complexity (whole ecosystem vs. single-species; Plagányi, 2007) and unit of measurement (biomass- vs. size-based; De Roos et al., 2003). While this review does not provide a comprehensive list of the existing simulation models, a broad overview of the main models for which IGP can be incorporated is addressed along with examples.

Multi-Species Individual-Based Models examine life cycle and impacts of targe. Individual-Based Models (IBM) consider the entire life cycle of an individual species and how its interactions impact ecosystem dynamics (Plagányi, 2007). To account for multi-species interactions such as IGP, IBM is expanded to form a multi-species individual-based model. OSMOSE, for example, simulates interspecific species interactions among fish of higher trophic levels via predation, under the assumption that predation is non-selective, dependent on the predator-prey size ratios and their spatiotemporal occurrence (Shin and Cury, 2001). OSMOSE has a hierarchical structure, with fish grouped by species, age-structure, size and weight, allowing for the study of species- and size-specific trophic interactions. The level of IGP can be simulated through the assessment of fish group movements across a closed-boundary, two-dimensional grid (Shin et al., 2004; Irigoien and De Roos, 2011).

A study by Andonegi et al. (2013) compared single-stock assessments of two economically important fish species from the Bay of Biscay, European anchovy, *Engraulis encrasicolus* and sardine, *Sardina pilchardus*, with predictions from several models, including OSMOSE. A size-based link was revealed between the anchovy population and eight other important species within the bay system including Atlantic mackerel, *Scomber scomber* and Atlantic bluefin tuna, *Thunnus thynnus*. Although the level of IGP between the sardine and anchovy was unknown, OSMOSE allowed investigation of possible direct and indirect effects of IGP through simulating different fish population sizes within the system. Results indicated annual variability in anchovy and sardine populations, whereby changes to the anchovy population dynamics were

directly linked to population changes in other fish species within the system, for example, mackerel and sardine (Andonegi et al., 2013).

Minimal realistic models limit the number of study species to a subset of the ecosystem. Minimal realistic models (MRM), or dynamic multi-species models, limit the number of species included by restricting the model to a subset of the ecosystem (Punt and Butterworth, 1995). Most simulation models are categorized as MRM including GADGET (Begley, 2005) and MULTSPEC (Bogstad et al., 1997) and capture IGP by including age-structured interactions (Plagányi, 2007). An age-structured MRM was used, for example, to improve the stock assessment of the South African hake fishery comprised of the shallow-water Cape hake, *Merluccius capensis* and the deep-water Cape hake, *M. paradoxus*. The hake species were known to engage in IGP and cannibalism, however, total allowable catch (TAC) was traditionally estimated using single-stock models that failed to include species interactions and food web dynamics (Ross-Gillespie, 2016). Intraguild predation was incorporated into the existing stock assessment model through the inclusion of an additional hake mortality parameter, predation by conspecifics. The MRM output reflected population oscillations, similar to those reported in the early 20th century when the development of the *M. capensis* fishery caused *M. paradoxus* populations to increase in response to predatory release. Modern populations of *M. paradoxus* have decreased and MRM predictions reflected a greater depletion than previous models had suggested. By including IGP and multi-species interactions into fish population assessments, more reliable data is available that can improve the sustainability, management and economic viability of fisheries (Ross-Gillespie, 2016).

Dynamic system models include external factors driving ecosystem function/structure. Dynamic system models account for the driving forces within an ecosystem, for example through top-down or bottom-up approaches and provide user control over external factors such as temperature and pH (Fulton and Smith, 2004; Condie et al., 2014). Typically restricted to a subset of species, these models focus on target species with greater detail than more complex modelling, such as whole ecosystem models (Plagányi, 2007). For example, ATLANTIS examines the response of 'network motifs', interconnected patterns within food webs that cannot be explained by chance, such as IGP that form trophic loops, to perturbations such as climate change and overharvesting (Fulton et al. 2004b & c). Small changes to closed loops have been shown to drive diverse responses that alter the direction and strength of predicted population trends, suggesting motifs heavily influence system functioning (Condie et al., 2014). When applied in a fisheries context, population recovery of the eastern gemfish, *Rexea solandri*, slowed despite fishery closures and historically low TAC (Little and Rowling, 2010). The unexpected ecological response was considered to be in response to strong IGP interactions between $IG_{predator}$ the arrow squid, *Nototodarus gouldi*, an omnivore that forages on IG_{prey} juvenile gemfish thus impeding its recovery (Condie et al., 2014).

Whole Ecosystem Models account for all trophic levels and interactions in a food web. Whole ecosystem models incorporate all trophic levels to form a three-dimensional model that captures the full structural complexity of food webs (Plagányi, 2007). Examples of whole ecosystem models include Ecopath with Ecosim (EwE v6.6.1; Ecopath International Initiative, 2020), bioenergetic, allometric and trophodynamic models (e.g. Koen-Alonso and Yodzis, 2005). Formed from the combination of Ecopath (Polovina, 1984; Christensen and Pauly, 1992), Ecosim (Walters et al., 1997) and Ecospace (Walters et al., 1999), EwE describes temporal changes in biomass between groups of species in response to complex interactions (Christensen and Walters, 2004) and can be used to study IGP (Walters and Martell, 2004). Ecopath estimates how changes in production and loss of species biomass, resulting from fishing activity, affect food web structure (Pauly et al., 1998). Ecosim (v2004; Entsminger, 2019)

incorporates temporal changes in initial system variables, such as species' life-histories or increases in IGP, and Ecospace is a spatially explicit model for fishing effort and biomass distribution (Walters et al., 1999).

Changes to food web structure in response to increased IGP among shark populations were measured by Kitchell et al. (2002) through a EwE of the Central North Pacific. The study performed two simulations: a baseline scenario and an apex shark scenario. The baseline scenario simulated the response of the food web to fishery management practices, such as longline fisheries, by including the trophic position of focal sharks as estimated from stomach content data reported in the literature. The apex shark scenario was simulated under the assumption that sharks play a greater top-down role than assumed. This was achieved by assigning large sharks with a higher trophic position value to reflect increased IGP through the consumption of elasmobranchs. Overall the apex shark scenario found by including a low level of IGP (i.e. 5% shark consumption), strong non-linear responses throughout the entire food web relative to limited effects observed from the baseline scenario (Kitchell et al., 2002).

There is a multitude of simulation models available that can be used in future IGP studies, with tradeoffs between model complexity and confidence in model results. Existing IGP models can act as a starting point for future IGP studies by providing a tool for improved realism when studying multi-species interactions. Model requirements may be difficult to meet, specifically when studying data-deficient target species. The selection of an IGP model will involve an examination of the available information and the model criteria. When possible, several different models may be used to avoid bias and misleading conclusions (Koen-Alonso and Yodzis, 2005).

3. The status of IGP studies after 30 years

The seminal IGP review by Polis et al. (1989) described the food web implications and broad suite of ecological effects of species involved in IGP. Here we used Polis et al. (1989) as a framework for a systematic assessment of the research effort conducted to date at three distinct IGP 'implication levels': i) individual, ii) population and iii) community. Though the implication levels were not defined by Polis et al. (1989), it is assumed that the individual level is the study of one entity, the population level examines characteristics among a group of individuals from the same species (Mendelian population; Dobzhansky, 1950), and community-level studies investigate characteristics of a network of multiple populations. Within each level, IGP can influence or be influenced by different characteristics, known as 'IGP effects' (Polis et al., 1989; Holt and Polis, 1997).

The status of current IGP knowledge was determined using a 'two-tiered approach' to ensure all existing studies were captured for each topic: i) a broad systematic search of existing literature on IGP using the terms 'intraguild predation' and 'cannibalism' (an intra-specific interaction), the implication-level, and synonyms for the IGP effects within the level, and ii) a narrower systematic search, including only the key terms specified in Polis et al. (1989); Fig. 4). The search results from i) and ii) were compared and results were found to be comparable providing confidence that the research effort was thorough (Fig. 4). IGP effects with more or less research effort are identified and recommendations are made for novel methods that can be used in future IGP studies to bridge knowledge gaps.

3.1. Individual-level implications

Interactions at the individual level operate as the biological building blocks for food web structure. Individuals may experience shifts in fitness, behaviour, morphology, chemical and life-history characteristics in response to IGP interactions that alter the stability and function of an entire ecosystem (Johnson, 2000; Finke and Denno, 2005). Additionally, several individual-level characteristics can facilitate an ideal environment for the occurrence of IGP (Nilsson-Örtman et al., 2014).
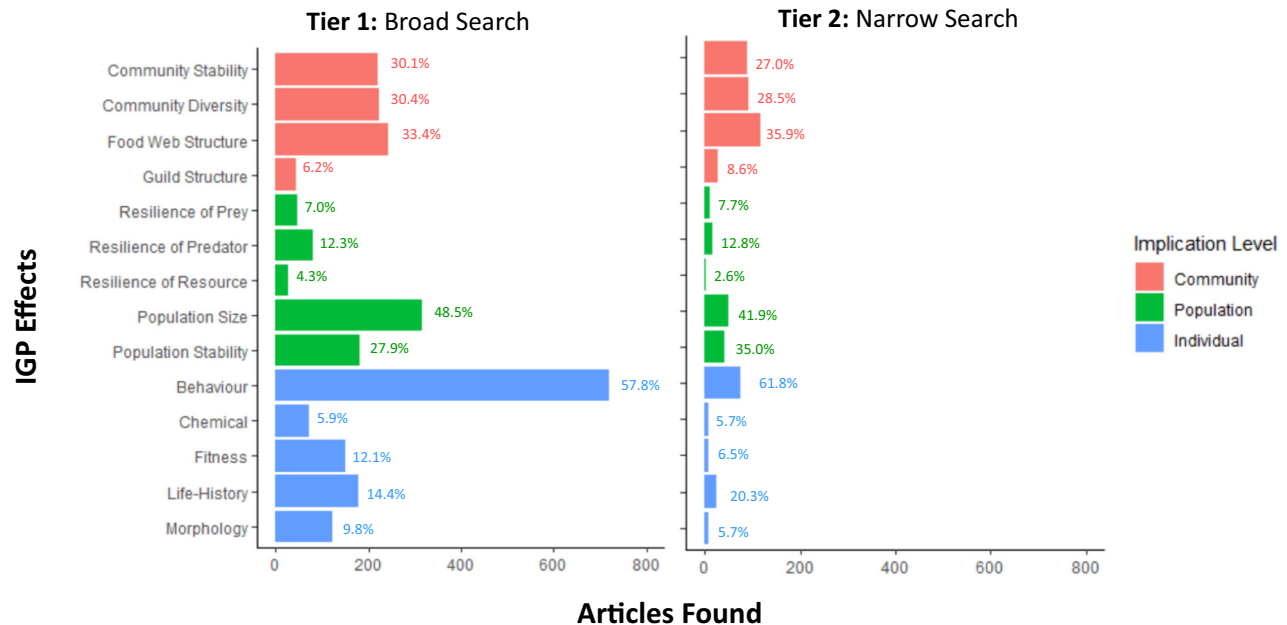
Literature Search Results

Fig. 4. Literature search results grouped by tier whereby Tier 1 is a broad overview search (N Tier1 = 2628) that includes key terms 'intraguild predation' and 'cannibalism' as well as the implication level and synonyms for the intraguild predation (IGP) effect. Tier 2 is a narrow search (N Tier2 = 566), removing 'cannibalism' and synonyms, using only the terms listed in the seminal work of Polis et al. (1989). The IGP effects from the Polis et al. (1989) paper are listed on the y-axis and each colour delineates the implication-level at which IGP effects can occur; the individual (blue; Tier1 n = 1244, Tier2 n = 123), population (green; Tier1 p = 653, Tier2 p = 173) and community levels (red; Tier1 c = 731, Tier2 c = 326). The percent of each IGP effect relative to the total number of search results for each implication level are provided at the end of each bar. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Many of the pioneering studies of IGP focused on observational changes to individual species traits to measure individual fitness levels and energetic gains acquired by the $IG_{predator}$ from the consumption of IG_{prey} (e.g. Walter, 1987). Effort is given to individual characteristics influenced by IGP, which vary considerably across studies, with behavioural changes in response to IGP (e.g. adaptive foraging; Wootton, 2017) the most frequently studied both at the individual level (n = 76, 62%; Fig. 4) and across all IGP effects combined (N Tier 2 = 566, 13%). Some examples of behavioural changes include changes in mobility of IG_{prey} (Lucas et al., 1998), spatial avoidance of $IG_{predators}$ by IG_{prey} (Tannerfeldt et al., 2002) and increased growth rate of $IG_{predators}$ (Takatsu and Kishida, 2015). By contrast, individual changes in chemical, morphological and fitness characteristics in response to IGP have received less study (5.5–6.5%, Fig. 4). Modern technological advancements and analytical methods, such as molecular tools, provide opportunities for increased understanding of IGP influences on species chemical traits (Thomas et al., 2013). Hautier et al. (2008) used gas chromatography–mass spectrometry analysis (GC–MS) to monitor IGP in coccinellid species via alkaloids, a defensive chemical produced to deter predation by ants (Marples, 1993), birds (Marples et al., 1989) and conspecifics (Glisan King and Meinwald, 1996). GC–MS can detect exogenous alkaloids, for example adaline, from IG_{prey} within the gut of an $IG_{predator}$ post-consumption, confirming the occurrence of IGP (Hautier et al., 2008, 2011).

3.2. Population-level implications

The outcome of interspecific interactions can have broad implications on species populations. When studying IGP at the population level, the size, stability and resilience of IGP species are examined (Fig. 4). Changes to population size in response to IGP (n = 49, 42%; Fig. 4) has been heavily studied in the literature, whereas minimal focus has been given to the resilience of IGP species (predator, prey

and resource) in response to IGP. The study of the resilience of a resource in response to IGP, for example, ranges from 2.6% (n = 3) at the population level to 0.5% (N Tier 2 = 566) across all implication levels (Fig. 4). Early IGP population studies focused on population size likely because it can be easily monitored via counts of individuals (Connell, 1983; Polis and McCormick, 1986). Studying changes in the resilience of a resource, for example, is not as straightforward as there is no simple metric for 'resilience'.

One area of study that has examined the effects of IGP on a common resource is through the biological control of agricultural pests (Finke and Denno, 2005; Frank, 2010). Pest species are typically herbivores, therefore crop yield and profit are dependent on the successful management of these species. Exotic predators introduced to consume a pest are often assumed to be safe provided they consume only the target pests (Sheppard, 2003), however, exotic predators may experience additional interactions, such as IGP with native predatory species, that can inhibit pest control and thus fail to reduce pest population density (Pearson and Callaway, 2005). For example, IGP interactions were found among predatory species used for pest control of the green peach, cabbage (Snyder et al., 2006), potatoes, (Lucas et al., 1998), grain (Sheppard et al., 2005) and milkweed (Lucas, 2005). Intraguild predation has also been observed among biological control species and plant pathogens (Martin and Hancock, 1987; Tixier et al., 2013). Although concentrated study effort has focused on pest control, few studies measure changes in the resilience of the pest in response to IGP, focusing instead on the success or failure of the biological control program, often through examining crop yield (Finke and Denno, 2005; Frank, 2010).

3.3. Community-level implications

Understanding IGP at the community level provides insight into changes to guild structure, community diversity, community stability

and overall food web structure (Polis et al., 1989). The response of food web structure to IGP has received the greatest research effort of the community-level IGP effects ($n = 117$; 36%; Fig. 4), while community stability and diversity have received a moderate level of study (27–29%; Fig. 4). The intense effort afforded to understand structural changes of food webs may coincide with growing concern over the impacts of biodiversity loss on ecosystems (Dirzo and Raven, 2003; Ceballos et al., 2015), and recent IGP studies have revealed stabilizing properties of moderate levels of IGP within communities (Rudolf, 2007; Miller and Rudolf, 2011). Consequently, IGP community-based models provide a promising approach for predicting food web responses to perturbations and to mediate additional loss of species diversity (Urbani and Ramos-Jiliberto, 2010).

Changes to the 'guild' structure, i.e. structural changes to the group of species in a community that use similar resources (Polis et al., 1989), is one IGP effect at the community level that has received minimal research effort ($n = 28$, 9%; Fig. 4). This knowledge gap may exist as several generations may be necessary before the observation of guild structure changes are detected (Briggs and Borer, 2005). The financial and logistical challenges of long-term monitoring often result in the use of short-term experiments to extrapolate long-term predictions (Brown et al., 2001; Hastings, 2004). Modern technological advancements provide increased opportunity to study long-term changes in IGP that are necessary to fully understand how species respond to climate change. For example, Yurkowski et al. (2017) used SIA to investigate changes in foraging patterns of an IG$_{predator}$ beluga (*Delphinapterus leucas*) on IG$_{prey}$ Greenland halibut (*Reinhardtius hippoglossoides*) in response to increases in abundance of a common resource, capelin (*Mallotus villosus*). The study identified an overall decrease in asymmetrical IGP across two decades resulting from a northward distribution shift of capelin with climate change (Yurkowski et al., 2017).

4. Conclusions

In the modern age of ecosystem-based studies, it is increasingly important to account for the total complexity of a food web when attempting to understand species interactions and their consequences. Intraguild predation does not account for all species interactions but, it incorporates several species across different trophic levels. For improved comparison among IGP studies, verification of essential interactions (i.e. competition and predation) and classification of IGP type (i.e. symmetry and age-structure) is encouraged. Diverse methods from qualitative direct observation to integrated telemetry and sensor approaches afford exciting opportunities to investigate the occurrence and strength of IGP in modern food webs.

Traditional IGP models demonstrated several population dynamics that occur when IGP is present in a food web, including coexistence, alternative stable states, competitive exclusion or instability of species populations. The possibility for the coexistence of IGP species, however, was assumed rare and unstable in traditional IGP models. Added realism, through the inclusion of model parameters, reconciled the discrepancy between empirical and theoretical studies, demonstrating the increased opportunity for IGP species coexistence. Improved resolution of IGP models, through growth from one dimensional to ecosystem-level frameworks in conjunction with more robust computer processing, is now providing methods for more accurate stock assessments in fisheries and improved management practices to ensure resource sustainability.

Future IGP research effort focused on chemical and morphological changes in individual-level IGP studies and the resilience of common resources to IGP at population and community levels is required. Rapid advancements in methodological approaches (such as compound-specific isotope analysis of individual amino/fatty acids), the continuing development of novel sensors (such as predation tags) and simulation modelling provide avenues for exploring IGP with opportunities to address knowledge gaps through sophisticated experimental designs. Interdisciplinary approaches will improve confidence in IGP study results, while modern multi-species modelling will progress the quantification of IGP in an ecosystem context. Through a multifactorial approach that accounts for system complexity, the study of IGP can better predict how food webs are and will respond to perturbations in turn improving our understanding of the underlying mechanisms responsible for ecosystem function.

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