The trophodynamics of marine top predators: Current knowledge, recent advances and challenges

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ABSTRACT

We review present understanding of the spatial and temporal diet variability (trophodynamics) of a range of pelagic marine top predators, at both early and adult life history stages. We begin with a review of methodologies used to advance our understanding of the trophodynamics of marine top predators, particularly in relation to climate change. We then explore how these developments are informing our understanding of the major trophic groups in food webs leading to, and including, marine top predators. We examine through specific examples how the impacts of ocean warming may affect pelagic food web relationships from both top-down and bottom-up perspectives. We examine the potential, in the absence of long-term data sets, of using large-scale spatial studies to examine how potential changes in biological oceanography could impact the biomass and composition of prey species, particularly the role of phytoplankton size spectra. We focus on examples from regions where biotic change with respect to climate change is likely. In particular, we detail the effects of climate change on oceanographic and bathymetric "hotspots" and provide the example involving seabirds in the Benguela Current system. We end by urging the development of international collaborations and databases to facilitate comprehensive ocean-scale understanding of climate impacts on marine top predators.

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1. Introduction

The dynamic processes of trophic interactions, or trophodynamics, leading to pelagic marine top predators[1] is a major focus of studies aimed at determining the impacts of anthropogenic- and climate-induced changes in marine ecosystems (Le Borgne et al., 2011). Although trophic interactions of many top predators are well documented, the dynamic component, that is the spatial and temporal variability, is less well described. This variability, beyond physiological requirements, is likely linked to the distributions, quality and quantity of prey. In broad terms, these prey are generally comprised of, but not limited to, a suite of small species collectively termed micronekton (size range 2–20 cm). Micronekton are distributed heterogeneously through the world's oceans, both horizontally and vertically, largely due to "bottom-up"

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  [1] Here we define top predators as a guild of large predators near the top of the food web, including seabirds, marine mammals, large pelagic fishes and sharks

processes forced by regional to basin-scale oceanography and bathymetry. At the basin-scale, for example, eastern boundary currents and their associated upwelling yield a predictable enhancement in production (hotspots) that can be important to top predator life histories and migration, while at finer scales, eddies (e.g. Lebourges-Dhaussy et al., 2009; Menkes et al., 2002) and fronts provide important oases in the open ocean (Godø et al., 2012; Lara-Lopez et al., 2012). Bathymetrically, features such as seamounts, islands and shelf breaks that present barriers to current flow or host high benthic production can also attract aggregations of top predators (Hyrenbach et al., 2000).

Climate change and its associated impacts are predicted to significantly affect the distribution and abundance of micronekton communities, and hence the predators they support, either directly or indirectly. Direct impacts may include horizontal and/ or vertical range shifts as a behavioural response to physiological constraints imposed by a change in temperature, currents, oxygen or pH levels. Indirect impacts include changes in the composition and productivity of the phytoplankton and zooplankton that constitute the base of the food web, and the micronekton prey communities. Basin-scale changes in phytoplankton biomass and zooplankton community structure have been observed in response to climate oscillations and long-term climate change (Beaugrand et al., 2009; Boyce et al., 2010; Olonscheck et al., 2013; Perry et al., 2004). Such changes have significant implications for the quantity and quality of prey available to micronekton and ultimately higher trophic levels.

Within increasingly sophisticated models developed to predict the response of marine ecosystems to environmental and anthropogenic changes, the complexity of trophic interactions are key for representing these changes (e.g. Ainley et al., 2007; Estes et al., 2011; Estes et al., 1998; Griffiths et al., 2013). Until now, most models have taken a bottom-up approach to food web structure, but have paid relatively little attention to low and mid trophic-level dynamics (cf. Watters et al., 2003). More recently, the importance of lower and mid trophic level interactions as food web drivers has increasingly been highlighted, either through closer examinations of primary or secondary producers (e.g. Griffiths et al., 2013; Kloser et al., 2009; Miller et al., 2010; Polovina et al., 2011; Polovina and Woodworth, 2012) or through explicit calls from modellers (Lehodey et al., 2010). Kloser et al. (2009) showed that ecosystem models have significantly underestimated the biomass of micronekton prey. In addition, the role of top down processes in structuring marine food webs is gaining increasing attention (Ainley et al., 2007; Cury et al., 2000; Nicol et al., 2007; Polovina and Woodworth-Jefcoats, 2013; Worm and Myers, 2003). The discussion of which of these processes, top-down or bottom-up, is more important has shifted to the understanding that both in concert are important contributors to fully understand how ecosystems respond to change. Both, however, are hampered by the lack of comprehensive long-term data sets, and spatial and temporal patchiness in data collection (Nicol et al., 2013). It is clear that more detailed food web information will be needed to improve predictions of the response of ecosystems to ongoing perturbations.

Climate change effects will potentially have the greatest impact in areas known as "hotspots". The term "hotspot" originated in the terrestrial literature and is defined as an area of high species endemism and a conservation priority (Myers et al., 2000). In marine ecosystems, particularly pelagic systems, the habitat underlying hotspots is particularly complex as it is created by oceanographic features that are highly dynamic in space and time. Additional criteria have been developed to classify marine hotspots including areas of low diversity yet high biomass, high biological productivity and high trophic transfer such as the temperate and polar seas (e.g. krill and krill consumers; Cotté

and Simard, 2005; Nowacek et al., 2011). Hotspots may also have a temporal component. In the Antarctic for example, humpback whales and their krill prey co-occur in "super-aggregations" in Antarctic bays in late autumn in a complex relationship tied to the extent of sea-ice from the previous winter. How the potential loss of sea ice through climate change, and its role as krill habitat, will impact Antarctic communities generally is a major research focus (Nowacek et al., 2011).

In this paper we draw on examples from a range of ecosystems and studies to summarise advances and challenges in food web research and explore how we might focus future studies to best support our understanding of present and future impacts of climate change on top predators. Specifically, we examine the main components of the pelagic food chain, and assess current knowledge in the context of top predators. Subsequently we suggest integrative approaches to bring the different disciplines together in whole food web analyses which can ultimately be used to inform models and ecosystem-based management practices.

2. Method development: techniques to support trophodynamics insight

Central to studies on trophodynamics are accurate measurements of predator–prey-relationships. Early accounts of trophodynamics of top marine predators were based on stomach content analysis and direct observations from ships or land colonies. As technology, biological understanding and numerical techniques have advanced, so has our capacity to assess top predator diets based on the analysis of biochemical compounds and deployment of acoustic tags. All approaches used to study trophic interactions of top-order predators have their own suite of advantages, limitations and current priorities (Table 1). Although the existing methodologies for dietary analysis have shortcomings, when used in combination, they provide powerful tools for trophic studies (e.g. Connan et al., 2014).

2.1. Stomach contents provides critical information on prey composition

Stomach content or scat analyses continue to provide a valuable source of information on predator–prey relationships. However, stomach content analyses are hamstrung by differential identification difficulties of prey items, e.g. rapid digestion/disintegration of gelatinous and other soft-bodied and small organisms, and the short-term dietary snapshot provided due to short digestion times. Nevertheless, high quality analyses of stomach contents are an essential part of food web understanding because they provide a high level of taxonomic context to predator–prey relationships not yet duplicated by other methods. The advent of new statistical methodologies permit the analysis of broad-scale spatial, temporal, environmental, and biological relationships in a classification-tree modelling framework and provide predictions of prey compositions of predators (Kuhnert et al., 2012; Olson et al., 2014). Identification of prey remains also provide the ground-truthing for many of the more contemporary methodologies that follow.

2.2. Biochemical tracers provide an analysis of diet integrated over time and space

Biochemical tracer techniques (e.g. stable isotope and fatty acid analysis) now provide well established methods for investigating trophic relationships that offer several advantages over stomach content analysis (Table 1). These techniques focus on assimilated versus ingested prey material, and can be used to identify food

Table 1
Summary of empirical methods used to study trophodynamics of top predators.

Methods	Applications (advantages)	Limitations	Future directions and priorities	Key references
Stomach contents	– High resolution taxonomic (species) description of diet composition – Consumption rate estimates can be obtained.	– Time consuming. – Large number of lethal samples required. – Differential digestion of prey groups leads to assessment bias.	-Continued effort to standardise the statistical treatment of stomach data (e.g. through using classification and regression trees; Kuhnert et al. (2012)).	Hyslop (1980)
Biochemical tracers (including: stable isotopes, fatty acids, compound specific amino acids, contaminants and trace elements, and molecular methods)	– Compounds altered in predictable ways -Improved trophic knowledge over time and space. – Different organism tissues can be used to investigate diet at different time (days to years) and biological (species to systems) scales. – Requires fewer samples than stomach content analysis; more cost-effective. – Can be non-lethal (using tissue biopsies, teeth, fish scales, hairs, etc). – Opportunity for retrospective analyses. – Provide physiological knowledge	– Taxonomic classification problematic. – Biochemical incorporation dynamics and metabolic turnover rates of tissues poorly understood. – Requires knowledge of an organism's key prey and their biochemical composition. – Often based on untested or unrealistic assumptions related to paucity of experimental studies. – Low predictive power. – Multiple sources with same signature.	– Advancement and standardisation of statistical methods. – Multi-tracer and combined tracer- telemetry approaches. – Knowledge on integration in tissues, fractionation and routing processes. – Understanding the dynamic state of body constituents. – More laboratory experiments.	Ramos & Gonzalez-Solis (2012), Layman et al. (2012), Hopkins and Ferguson (2012), Budge et al. (2006), Parrish (2013), Masbou et al. (2013), Germain et al. (2013), Pompanon et al. (2012)
Telemetry (or electronic-tagging)	– Mapping distribution. – Estimates of where and when a predator interacts with prey. – Real time accounts of organism movement patterns and environmental conditions.	– Expensive (limits sample sizes). – Assumes that short-term, individual behaviour reflects population mean. – Unable to deploy on small or gelatinous organisms due to weight constraints or resolution of loggers.	– Miniaturisation of sensors and instrumentation to widen usage. – Increase longevity of batteries so that long time-series data can be collected. – Refinement of statistical methods.	Evans et al. (2012), Papastamatiou et al. (2013), Hazen et al. (2012), Hindell et al. (2010)

web sources, which cannot be achieved through stomach content analysis. Depending on the tissue type and the biochemical compound analysed, dietary information is integrated over periods of days to years. Trophic information can be acquired from preserved soft and hard tissues (e.g. hair, bone, muscle tissue, beaks, scales, otoliths, feathers) and thus enable retrospective analyses using archived material. For species of conservation concern, new material for biochemical analysis can also be collected by non-lethal methods, such as taking hair follicles from mammals, feathers from birds and a skin graft or muscle biopsy from fishes. Just as biochemical techniques have similar applications, they also share limitations (Table 1). These include a poor understanding of the influence of metabolic processes on biochemical signatures and a paucity of data across the wide spectra of potential prey of marine top predators. Advancement of statistical and numerical techniques, and compilations of large datasets (e.g. for meta-analysis) is currently at the forefront of utilising ecological data acquired from biochemical tracers. Here we explain some features of the main biochemical techniques used to understand top predator trophodynamics.

A critical step in assessing trophic interactions is the accurate measurement of an organism's trophic position[2]. The trophic position represents an extremely powerful metric when

examining regional variation and long-term change (e.g. response to top-down and bottom-up forcing) and is a fundamental parameter for most ecosystem models. Central to estimating stable isotope-based trophic position is the measurement of the isotopic signature of the trophic baseline, usually a measurement of the $\delta^{15}N$ values of phytoplankton or particulate organic matter (Lorrain et al., 2015). Lorrain et al. (2015) provide an overview and assessment of methods, comparing estimates from primary producers, primary consumers, and amino acid compound-specific isotopic analysis (AA-CSIA). Once baseline isotope values are established, indices such as trophic position, food-chain length and transfer efficiencies can be estimated (Hunt et al., 2014; Olson et al. 2010); these present a powerful means for comparing among regions (e.g. Choy et al., 2012) and time periods. The application of stable isotopes to identifying food-web connections has been greatly improved by the development of Bayesian mixing models (Jackson et al., 2011; Moore and Semmens, 2008; Parnell et al., 2010). Initially developed to identify the relative contribution of dietary sources to a single consumer, recent developments provide

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[2] Following Post et al.'s (2000) terminology, we consider "trophic position" as a continuous measure as opposed to discrete "trophic levels."

insights into whole food web interactions (Kadoya et al., 2012). The potential of AA-CSIA is particularly evident for archival samples, for which information on past isotopic values of the baseline is rarely available, as it allows comparison of environmental vs. trophic effects in the same sample (e.g. Sherwood et al., 2011).

Nitrogen isotope signatures can be used as tracers of both trophic pathways and geographical movements of top predators and their prey (Popp et al., 2007). They have also been used to ground-truth dynamic ocean habitats (Hobday et al., 2011). Identification of global spatial patterns in the nitrogen isotope values of baseline nutrients (e.g. Somes et al., 2010) allow for the application of nitrogen isotope measurement of bulk tissues to infer trophic niches of widely distributed consumers (Navarro et al., 2013). Carbon isotope signatures are strongly driven by ocean temperature and can therefore be used to infer feeding locations of migrating species (Mendes et al., 2007; Witteveen et al., 2009). Additionally, carbon isotope signatures of individual amino acids is developing as a new tool to trace the biosynthetic sources of carbon in higher-order consumers (Arthur et al., 2014; Larsen et al., 2009).

Whereas stable isotopes have the advantage of supplying a simple indicator of relative trophic position or spatial differentiation, signature fatty acids (SFAs) can be used to broaden that understanding using the complex of dietary-derived fatty acids that make up adipose tissues (Pethybridge et al., 2013). The technique is based on the fact that dominant organisms at the base of the food chain have distinct fatty acids profiles that are transported, relatively unmodified, to high-order predators (Parrish 2013). Parrish et al. (this issue) found characteristic SFAs separating tropical and temperate populations of albacore tuna (*Thunnus alalunga*) in the western Pacific Ocean, suggesting that this method may have a broader role in distinguishing populations generally. At larger ecological scales, changes in the bioavailability of certain (dietary essential) fatty acids has been related to climate-induced community transitions in boreal oceans (Litzow et al., 2006). In addition to gaining key trophic information on given species, lipid content of tissues have been shown to provide a powerful method for assessing energy transfer in individual species and marine ecosystems (Pethybridge et al., 2014).

Another biochemical approach used to investigate the feeding ecologies of top marine predators is the analyses of trace elements and metals that accumulate in the hard and soft tissues of top predators (Ramos and Gonzalez-Solis, 2012). Persistent inorganic (e.g. cadmium), and organic (e.g. PAHS, PCB, and pesticide) compounds, along with trace metals (e.g. methylmercury), have proven very useful, largely due to their high transfer from prey to predator, high absorbability once in the gut, and limited ability to be metabolised. These compounds can be used to indicate anthropogenic contamination, such as lead from leaded gasoline and hydrocarbons from oil spills. In feeding studies, they can be used to show a specialised diet or feeding habitat, such as the consumption of deeper-dwelling prey based on mercury levels (Choy et al., 2009) and the consumption by cephalopods using cadmium (Bustamante et al., 1998).

Stable isotopes of mercury (δ^{202}Hg and Δ^{199}Hg) are retained in organisms up to top predators (Point et al., 2011), and they add value to traditional carbon and nitrogen isotope methods as food web tracers, while also providing information on foraging depth (Blum et al., 2013) and/or inshore-offshore differences (Senn et al., 2010). New developments for Hg compound-specific stable isotope analysis (Hg-CSIA; Masbou et al., 2013) coupled with Hg SIA could become a standard part of the isotope toolbox for more general trophic studies.

Molecular methods offer a rapid, unambiguous alternative to visual identification of species present in gut contents (King et al., 2008). Prey species-specific based assays can be designed to detect the presence of these prey in a range of potential predators (Albaina et al., 2010; Albaina et al., 2012). The application of such molecular

techniques can provide a rapid screening of a large number of potential predators for a given prey taxon. This can include critical stages such as eggs and larvae, that are otherwise difficult to identify visually in predator stomachs, and provide a more holistic description of the predator community (Fox et al., 2012). On the other hand, the application of DNA barcoding in diet studies of predators has increased considerably with the advent of next-generation sequencing technology (Pompanon et al., 2012). There is also potential for DNA metabarcoding approaches to resolve the importance of gelatinous and other soft-bodied organisms in marine food webs. Ongoing, large scale DNA barcoding initiatives (www.barcodeoflife.org) will be helpful to develop reference databases with the barcodes of all the potential prey species.

2.3. Telemetry allows organism habitats to be mapped and feeding inferences made

Observing movement and behaviour in marine top predators has been revolutionised by new telemetry technology (Evans et al., 2012). Telemetry informs trophodynamics in two ways: (1) the spatial locations of animals at-sea and the depth ranges they frequent, providing insight into habitat requirements and sometimes inference about prey type, and (2) some devices provide direct observation of prey capture, although the exact composition of the prey is rarely directly observed. Cameras carried by animals also allow direct observation of prey type and prey-capture frequency (Davis et al., 2013; Madden et al., 2008). Novel sensors such as jaw-gape sensors have allowed direct observation of feeding frequency. Miniaturisation of sensors and instrumentation is likely to widen the use of such methods (Davis, 2008).

Patterns of acceleration (e.g. Goldbogen et al., 2013) and changes in stomach temperature also indicate ingestion processes in marine mammals (see review by Hindell et al., 2010) and other large predators such as lamnid sharks and tunas (Bestley et al., 2010; T. Clark et al., 2010; Goldman, 1997; Stevens and McLeese, 1984). Such information allows the relative buoyancy of the animal to be estimated, and therefore body-condition can be tracked over time (Biuw et al., 2003). For example, marine mammals were simultaneously equipped with satellite tags, time depth recorders and head-mounted accelerometers in the Austral Ocean, allowing accurate determinations of the number and 3D position of prey-encounter events (Guinet et al., 2014). Biuw et al. (2007) related changes in condition to large scale oceanographic features from a circumpolar telemetry data set.

Many telemetry studies collect location-only information. Inferring foraging effort from such data requires statistical approaches (e.g. McClintock et al., 2013). The most mature of these is the behavioural switching models estimated in a state-space modelling framework. Jonsen et al. (2012) provides a non-technical overview. Briefly, these models decompose animal movement data into resident phases, when an animal may be concentrating its foraging efforts in a small spatial domain, and transit phases, when the animal is moving rapidly between foraging patches. This class of modelling methods has been widely applied to fish (Patterson et al., 2009; Pedersen et al., 2011), turtles (Jonsen et al., 2007), seabirds (Dean et al., 2013), cetaceans (Pomerleau et al., 2011), and pinnipeds (Breed et al., 2009). A recent study by Dragon et al. (2012) has made favourable comparisons between statistical classification of behaviour with drift-rate estimation of increased condition in southern elephant seals (*Mirounga leonina*). Details of telemetry studies relevant to specific top predator groups are highlighted below.

3. Food web components leading to top predators

Pelagic predators are directly influenced by any changes in their micronekton food sources, which are in turn dependent on

Table 2
Main trophodynamics processes in relation to key trophic groups.

Ecological processes	Trophic Groups	Literature
a. b. c.	Phytoplankton	Acevedo-Trejos et al. (2013), Polovina & Woodworth (2012) and Uitz et al. (2010)
	Zooplankton	Atkinson et al. (2012), Fortier et al. (1994), Sommer and Stibor (2002) and Woodd-Walker et al. (2002)
	Micronekton	Brodeur et al. (2003), Lara-Lopez et al. (2012) and Robinson et al. (2010)
	Gelatinous	Hay (2006), Pitt et al. (2009), Purcell (2009) and Richardson et al. (2009)
	Crustaceans	Hopkins et al. (1994) and Boudreau and Worm (2012)
	Small pelagic fishes	Kloser et al. (2009) and Pakhomov et al. (1996)
	Cephalopods	Young et al. (2013) and Navarro et al. (2013)
	Seabirds	Duffy and Jackson (1986) and Barrett et al. (2007)
	Marine mammals	Pierce and Boyle (1991) and Pauly et al. (1998)
	Large predatory fishes	Menard et al. (2000), Pusineri et al. (2008) and Young et al. (2010)
	Sharks	Cortés (1997); Wetherbee (1990)
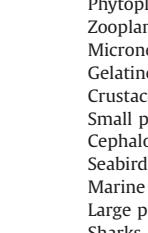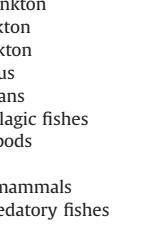
Ecological processes: (a) bottom-up where a large biomass of low-trophic organisms control the biomass of higher order predators; (b) intermediate (waist-wasp) where large biomasses of a few important mid-trophic organisms control the biomass of both their prey and predators; (c) top-down controls on lower trophic groups come from a high biomass of top predators.

the trophic levels below them (zooplankton and phytoplankton), i.e., bottom-up driven (Table 2). As the plankton are strongly impacted by climate variability (Atkinson et al., 2004; Hays et al., 2005; Martinez et al., 2009; Perry et al., 2004) and climate change (Bopp et al., 2001; Hays et al., 2005; Richardson, 2008), these processes are likely to be key drivers of micronekton biomass and species composition. Micronekton are also influenced by their predators, e.g. tunas and other large pelagic fishes (top-down processes), which in turn are impacted by fisheries (Polovina and Woodworth-Jefcoats, 2013). The micronekton themselves act on the trophic levels above and below, i.e. wasp-waist control, through variations in biomass (bottom-up) and predation (top-down) respectively (Cury et al., 2000; Griffiths et al., 2013). Although the importance of micronekton in pelagic food webs is unquestioned, understanding the dynamics of their role is hindered by knowledge gaps of their life histories, vertical distributions, quantitative biomasses, and diets (PICES, 2005, 2010). Inefficient and inconsistent sampling methods (e.g. midwater trawls of different designs, acoustics), and the undersampling of the vertical distribution of many micronekton species contribute to these data gaps and likely a significant underestimate of their global biomass (Irigoien et al., 2014; PICES, 2010).

3.1. Plankton size structure dynamics and energy transfer to top predators

Phytoplankton primary producers represent the base of the pelagic marine food web, and zooplankton grazers, dominated by copepods (Ryther, 1969), are the essential intermediaries between phytoplankton and higher trophic levels (Table 2). Phytoplankton can broadly be grouped into three size classes, pico (<2 μm), nano (2–20 μm) and microphytoplankton (20–200 μm) (Sieburth et al., 1978), representing a three-order of magnitude range in the prey field available to herbivorous zooplankton grazers. Most zooplankton, including copepods, cannot efficiently graze pico-sized particles (Fortier et al., 1994), necessitating an additional trophic step of microzooplankton grazers, e.g. ciliates (Sommer et al., 2002). In food webs with picophytoplankton as the dominant components of the primary production, approximately 50% of the autotrophic energy that enters the "copepod pathway" occurs via omnivorous feeding on microzooplankton rather than direct grazing (Calbet et al., 2005; Calbet and Saiz, 2005). In contrast, $\sim75\%$ of this energy enters the "copepod pathway" via direct phytoplankton herbivory in areas where microphytoplankton dominate.

Following the theory of size-structured predator–prey interactions (Cohen et al., 1993), the relative contribution of the pico- to microphytoplankton spectrum to a food web is expected to influence the size of the zooplankton grazers present. Small

copepods (<1 mm) generally dominate in systems with a low microphytoplankton contribution, while large copepods (>2 mm) and herbivorous euphausiids dominate in systems with a high microphytoplankton contribution (Beaugrand et al., 2003; Beaugrand et al., 2008; Conversi et al., 2010; Conversi et al., 2009; Hopcroft et al., 2001; Longhurst, 1998). The food chains resulting from the two ends of the phytoplankton size spectrum can differ in length by at least two trophic levels:

1. Picophytoplankton→Microzooplankton→Small   Copepod→ Carnivorous Zooplankton→Micronekton→Nekton
2. Microphytoplankton→Large Copepod / Euphausiid→Micro- nekton→Nekton

Since approximately 90% of the energy is lost from one trophic level to the next through respiration, excretion, and export processes (e.g. vertical flux; Cohen et al., 2003; Kerr and Dickie, 2001), differences in food chain length resulting from the size structure of the primary producers have significant implications for the efficiency of energy transfer to top predators (Dickman et al., 2008; Post, 2002). An additional feature of picophytoplankton-dominated food webs is that they favour the transfer of energy along a second, "jellyfish" trophic pathway (Sommer et al., 2002), through either direct grazing on the pico size fraction by tunicates (Fortier et al., 1994) or efficient predation by cnidarians and ctenophores on small zooplankton (Purcell, 2012). This gelatinous pathway has generally been considered to make little contribution to fisheries, effectively representing a "trophic dead end" (Hay, 2006; Richardson et al., 2009; Sommer et al., 2002; Verity and Smetacek, 1996). As highlighted below, there is growing evidence that this is not the case.

The drivers of phytoplankton size structure are therefore a necessary consideration to understanding present day food web dynamics and their potential responses to climate forcing and other ecosystem perturbations. Globally, picophytoplankton dominate in oligotrophic and nutrient-rich regions that are light and/or iron limited, while microphytoplankton dominate in naturally eutrophic regions that are light and iron replete (Ben Mustapha et al., 2013; Kiorboe, 1993; Uitz et al., 2010). Natural nutrient availability is largely determined by the physical processes that control vertical mixing and nutrient re-supply to the photic zone (Kiorboe, 1993). Climate induced changes in stratification, mixing, and ocean currents, therefore, represent important potential drivers of temporal shifts in phytoplankton size structure. There is already evidence for a decline in phytoplankton cell size in the sub-tropical oceans (Polovina and Woodworth, 2012), and long-term model projections are for this decline to continue with ongoing ocean warming and intensification of stratification in

the euphotic zone (Polovina et al., 2011). Significant positive correlations between temperature and increased picophytoplankton abundance observed in the north Atlantic indicate that temperature alone can be an important driver of phytoplankton size (Moran et al., 2010). Anthropogenic eutrophication in coastal regions is another driver, with associated enhanced Nitrogen:Phosphate ratios favouring the development of ciliates over diatoms and an overall reduction in plankton community size structure (Nagai, 2003; Purcell, 2012; Richardson et al., 2009; Uye, 2011).

3.2. Micronekton

Micronekton (including gelatinous taxa, crustaceans, small fishes and cephalopods), are generally distributed in the upper 1000 m of the water column (Kloser et al., 2009) where they are the main prey of most pelagic predators (Young et al., 2010). The micronekton themselves span a wide range of feeding modes, from herbivorous, to omnivorous and carnivorous, and they act as critical intermediaries in the size continuum of pelagic food-webs, between lower trophic levels and top predators (Hunt et al., 2014). As many micronekton species are deep migrators, they also play a key role in linking the epipelagic and mesopelagic food webs of the world's ocean, while also contributing to vertical carbon flux. The lack of knowledge on the trophodynamics of the micronekton is a continued impediment to fully understanding the role of this group in pelagic food webs, and their response to both bottom-up and top-down forcing (Olson and Watters 2003; Watters et al. 2003). In addition to dietary studies, an improved knowledge of the composition, distribution and biomass of the micronekton is also essential.

It is increasingly thought that the micronekton are under-sampled by traditional net systems (by up to an order of magnitude; Kaartvedt et al. 2012). Acoustics is beginning to provide improved information on the large spatial scale distribution and relative biomass of the micronekton, but more development is required to transform acoustic signals into estimates of absolute biomass (Handegard et al., 2013; Kloser et al., 2009; Menkes et al., this issue). However, the need for data on micronekton diets, and horizontal, vertical (epipelagic/mesopelagic), and temporal (diel and seasonal) dynamics of taxonomic composition, requires the improvement and standardisation of existing sampling methods (nets, stomach content examination of predators), which only give a partial view of the micronekton (due to avoidance and selectivity of the sampling gear and predators). Comprehensive stomach sampling from wide-ranging, generalist predators with high energy requirements is thought to provide less biased representations of micronekton composition than nets (Olson et al. 2014).

Recommendations from the micronekton inter-calibration experiment (PICES, 2010) highlight the gears and methods that most effectively sample the micronekton. Importantly, there is a requirement for consistency in the sampling methods applied in future micronekton studies, to generate more comparable and standardised estimates of global biomass. There is also a need for better classification of micronekton guilds or functional groups (Lehodey et al., 2010), to improve the incorporation of this group into both food-web and biogeochemical models. Comparative, observational approaches using historical data provide an additional data source for micronekton (Francis and Hare, 1994; Olson et al., 2014), while the development of new sampling methods (for example based on video and image analyses/optical systems) also hold promise for the gelatinous component in particular (Robison et al., 1998).

3.2.1. Gelatinous organisms

Within this group we include the subphylum Medusozoa (including Scyphozoa, Hydrozoa, and Cubozoa), Ctenophora and Thaliacea (including salps), and together they comprise probably the least well known micronekton. Gelatinous taxa span a wide range of size classes, from mesozooplankton of ~2 mm (e.g., some appendicularians), through micronekton (e.g. many salp species) to nekton (e.g. the > 1 m diameter scyphozoan *Nemopilema nomurai*). Together they cover a range of trophic levels; including primary consumers, such as salps that can graze up to 100% of daily phytoplankton production and complete with other grazers (Hereu et al., 2010; Pakhomov and Froneman, 2004; Perissinotto and Pakhomov, 1998); to carnivorous species such as *Mnemiopsis leydii* and various Scyphozoa that compete with fish and other micronekton for prey (Daskalov, 2002; Moller, 1984; Purcell and Grover, 1990; Purcell and Sturdevant, 2001). These interactions can both stimulate trophic cascades, e.g. through introduction of invasive species, and be caused by them, e.g. through overfishing (Daskalov, 2002; Lynam et al., 2006; Richardson et al., 2009).

Certain top predator species are known to specialise on gelatinous prey, e.g. the leatherback turtle. Stomach content analysis of opah (*Lampris guttatus*) and longnosed lancetfish (*Alepisaurus ferox*) found that gelatinous pyrosomes and salps contributed upwards of 20% by wet weight to the diet of these species (Choy et al., 2013). A review of the topic has shown that a large array of invertebrates, fishes and seabirds consume gelatinous prey (Arai, 2005). However, a common perception remains that gelatinous organisms represent a dead-end in marine food webs due to their low caloric value ($\sim$ 0.1 KJ g^{-1} wet mass in Doyle et al., 2007; Sommer et al., 2002). It is possible that stomach content analysis has systematically underestimated the consumption (and energetic contribution) of gelatinous organisms by pelagic predators due to rapid gastric evacuation and the difficulty in identifying partially digested gelatinous prey items. A recent study adopting a stable isotope approach indicated that gelatinous plankton may be a major dietary component of top predator species such as tuna and swordfish (Cardona et al., 2012). The rapid advancement of DNA barcoding methodologies provides an additional means to identify stomach contents, and these data can be used to validate stable isotope studies, such as the one above.

Increasing evidence suggests that the biomass of gelatinous organism has been on the rise globally (Brotz et al., 2012; Hay, 2006; Purcell et al., 2007). The potential causes of these observed increases include overfishing and trophic cascades (Gershwin, 2013; Roux et al., 2013), eutrophication (Purcell, 2012), and climate change (Atkinson et al., 2004; Purcell, 2012). Increases have also been linked to large scale, long-term climate oscillations (Brodeur et al., 2008; Condon et al., 2013). Recent studies have demonstrated that gelatinous organisms are physiologically well-adapted to take advantage of ecosystem disturbances (Acuña et al., 2011; Pitt et al., 2013), and this, in light of the evidence for increases, highlights improved quantification of their contribution to marine food webs as increasingly important (Brotz et al., 2012; Purcell, 2012; Richardson et al., 2009). The fundamental implications of anthropogenic-related increase in gelatinous organisms (Lilley et al., 2011) to the ecology of top marine predators, particularly in terms of their ability to acquire sufficient energy for growth and reproduction, needs further exploration. New biochemical tracer methodologies provide improved power to do so.

3.2.2. Crustacea

Micronekton crustacea such as pelagic crabs, crab megalopae, euphausiids, stomatopods, amphipods and decapods can dominate the diets of pelagic top predators, from temperate to subtropical regions (e.g. Goñi et al., 2011; Potier et al., 2007), in eastern boundary current upwelling zones (Miller et al., 2010), and in polar

regions (e.g. Cornejo-Donoso and Antezana, 2008). Herbivorous crustaceans, euphausiids in particular, are adapted to feeding on the larger, diatom dominated size classes (Fortier et al., 1994) found in eutrophic ocean regions, and are therefore able to take advantage of the high primary productivity, e.g. in upwelling systems (Perez and Sulkin, 2005). As described in Section 4.1., direct predation on large euphausiid diatom grazers by various nekton and other top predator species represents a highly efficient transfer of energy through short food chains. Changes in phytoplankton size structure due to climate change, therefore, have significant implications for the transfer of phytoplankton productivity to higher trophic levels via crustacean pathways. The role of deep pelagic shrimps species (particularly sergestid, mysid, penaeid and caridean taxa), many of which undergo extensive diel migrations, may also be underestimated in pelagic ecosystems (Flock and Hopkins, 1992; Karuppasamy et al., 2006; Kikuchi and Omori, 1985; Omori, 1983).

3.2.3. Small pelagic and mesopelagic fishes

Forage fishes (such as sardine, anchovy, and herring) and lanternfishes are key components of the epipelagic and mesopelagic communities, respectively. They are the major predators of copepods, euphausiids, ostracods and amphipods (Espinoza et al., 2009; Young and Blaber, 1986) and are therefore an essential step in the conversion of primary productivity to top-predator biomass (Table 2). Small fishes are critical to pelagic food webs, as they are fed on directly (Flynn and Paxton, 2012; Polovina, 1996) and indirectly (Menard et al., 2000) by most pelagic predators. Assessment of the lipid dynamics of small forage fishes have been related to local feeding conditions (Røjbek et al., 2013) and to secondary and stock productivity (Shulman et al., 2005). There is a vast literature on their ecology but determining their overall contribution to the pelagic ecosystem via ecosystem models (Fulton et al., 2005) is hampered by uncertainty in estimating their biomass (Kloser et al., 2009; Zwolinski et al., 2012). Acoustic estimates suggest that the biomass of this group may have been underestimated by an order of magnitude (Irigoien et al., 2014). Recent studies have concentrated on evaluating their spatial, temporal and trophic variability (Choy et al., 2012; Flynn and Kloser 2012), necessary components for developing secondary production models to provide a clearer understanding of top predator–prey fields and how they might respond to a changing climate.

3.2.4. Cephalopods

The cephalopods are an important prey for many top predators such as fishes, sharks and marine mammals (Young et al., 2013). Squids feed primarily on lanternfishes (Parry, 2006), and thus play a role in converting the massive biomass of small micronekton fishes to prey more suitable for a range of top predators. A recent review of the role of squids in pelagic ecosystems identified significant gaps in research (Young et al., 2013). Even though cephalopods are a major component of many ecosystem models, at least one sensitivity analysis indicated that they exerted the greatest influence of all the component groups on the eastern Pacific pelagic ecosystem, yet the cephalopods were among the least understood components of the model (Olson and Watters, 2003). Like other invertebrate groups, data on squid are relatively scarce when compared to fishes (Costello et al., 2010). However, more recent studies are beginning to provide a clear picture of not only their role as prey but also as predators within the pelagic ecosystem (e.g. Coll et al., 2013). Cephalopods, along with gelatinous zooplankton, are likely to be net "winners" from climate change (Griffiths et al. 2010; Rodhouse 2013). The dramatic rise in biomass of the Humboldt squid (*Dosidicus gigas*) in the eastern Pacific Ocean may be an extreme example of their potential adaptation to changing oceanographic conditions, in their case a possible response to the shoaling of the oxygen minimum zone (Stewart et al., 2013). A recent decrease in their biomass, however, suggests there may be other reasons for these fluctuations.

3.3. Early life history feeding of top predators

When comparing and evaluating the trophodynamics of the oceans' top predators, it has been common practice for researchers to limit their analyses to the adult stages. Many top predators undergo distinct morphological changes and dramatic growth in size early in life. It is widely acknowledged that, as for adults, early life stages of large marine organisms differ vastly in their trophic roles from one species to another (e.g. fish larvae versus recently-weaned toothed whales). More importantly, there can be major intra-specific ontogenetic shifts in feeding behaviours (e.g. the feeding of millimeter-scale teleost fish larvae versus that of the adults). For some species, including sharks, sea turtles, and, most notably, teleost fishes, such drastic changes in feeding ecologies lead to the early life stages representing trophically distinct members of the greater food web relative to their adult counterparts. Ideally, the early life stages of top predators should receive separate consideration to allow for a clearer understanding of the trophic interactions in the ocean, yet such considerations are rare.

The majority of our knowledge on the feeding dynamics of the early life stages of top predators centres around bony fishes. A reason for this may be that some groups have offspring with similar diets and feeding behaviours to the late-juvenile and adult stages. Many marine mammals, for instance, once weaned from their mother, will generally forage on the same resources as the adults. However, some evidence suggests that weaning calves of some toothed whales feed on different (slower and smaller) prey than do their older counterparts (Gannon et al., 1997; Smith and Read, 1992). Fledgling, independently-feeding sea birds also typically forage on the same prey as do the older juveniles and adults, but diets can sometimes differ (additionally, foraging success and efficiency commonly differ greatly among life stages in birds (Marchetti and Price, 1989)). Spatial considerations are also important, as the habitats occupied by the early life stages can be entirely separate from the predominant foraging grounds of the adults (e.g. Block et al., 2001; Bush, 2003; Reich et al., 2007), so the different stages of the same species may not even be part of the same food web.

All large pelagic teleosts spawn pelagic eggs, which hatch into planktonic larvae at ca. 2–3 mm in length and grow to tens of millimetres before gradually taking on the juvenile form and becoming entirely nektonic. Unlike adults, these larvae and early juveniles consume tiny prey (zooplankton and other fish larvae) to fuel their growth. Moreover, the early life stages are unique, in that they must face a wide range of predators. In fact, predation mortality including cannibalism (Young and Davis 1990), rather than starvation, likely represents the greatest source of larval fish mortality in the open ocean (Bailey and Houde 1989 but see Margulies 1993). Jenkins et al. (1991) reported density-dependent growth in larval tunas, indicating food limitation may also be important. Our knowledge of early-life trophodynamics of teleost top predators is largely limited to the larvae of select species of tunas, mackerels and billfishes (e.g. Catalán et al., 2011; Llopiz and Cowen, 2008; Llopiz et al., 2010; Morote et al., 2008; Sanchez-Velasco et al., 1999; Uotani et al., 1990; Young and Davis, 1990; reviewed by Llopiz and Hobday, 2015). For most of the remaining large pelagic teleosts (e.g. snake mackerels, escolars, cutlassfishes, molas, lampriforms, and louvar), sharks, rays and mammals, there

is little known about any aspects of their early life history, much less their feeding ecologies.

From what we do know about the feeding dynamics of larval and juvenile tunas and billfishes, some interesting behaviours and patterns have emerged. Larval diets of these taxa are often narrow —a function of highly-selective feeding behaviours—and, for a given species, they can be consistently similar at different locations around the world (Llopiz and Hobday, 2015). There are also regional differences in prey types and feeding success for some species of larval tunas, raising the possibility that spawning locations of tunas may vary in the degree to which they nutritionally support larval growth and survival. Pelagic tunicates such as appendicularians are consumed by some tuna species (and not others), to the complete exclusion of other zooplankton prey (Llopiz et al., 2010; Young and Davis, 1990), and it appears that almost all scombroid species become piscivorous as larvae (i.e. feeding upon other larvae), though the size at which this ontogenetic diet shift begins varies by species (Llopiz, 2013). Research on early juveniles has been limited to a handful of efforts on tunas, largely consisting of gut-inspection studies that found that small fishes, especially fish larvae, dominate as prey items (Aoki, 1999; Sinopoli et al., 2004; Tanabe, 2001). The dietary and spatial differences between larval/juvenile and adult forms of many top predators are an important consideration in understanding species response to changing ocean conditions.

3.4. Top predator trophic groups

3.4.1. Seabirds

Seabirds breed on land, but forage at sea, consuming globally a total of approximately 100 million tons of seafood annually, the equivalent of the annual landings of fisheries (Brooke, 2004; Karpouzi et al., 2007). Seabirds are distributed worldwide and forage in coastal and pelagic waters on a variety of species captured near the surface or deep in the water column. They capture prey by plunge-diving, pursuit-diving, dipping, skimming, pattering, surface seizing and scavenging (Shealer, 2001). Seabirds feed at a range of trophic levels: on zooplankton, large crutaceans (like krill) and small to medium-sized fish and squids (Shealer, 2001). Seabirds, like pelagic fishes, are gape-limited, hence they do not capture large prey. Exceptions to this are scavengers (e.g. wandering albatross, *Diomedea exulans*), which may tear pieces of flesh off large carcasses (Croxall and Prince, 1994).

Most knowledge of seabird foraging behaviour, foraging areas and diet originates from direct at-sea observations, stomach contents or regurgitation pellets collected at breeding colonies and bird kills (Barrett et al., 2007). As for other groups of marine top predators, the development of new technologies, particularly miniaturised electronic activity recorders (Ropert-Coudert and Wilson, 2005), is transforming radically our perception of the relationship between seabirds and their prey. Satellite tags, GPS and geolocators deployed on seabirds show how animals exploit physical oceanographic features, like eddies or fronts, which concentrate prey (Bost et al., 2009; Tew Kai et al., 2009), or travel thousands of kilometres over their annual cycle, visiting areas with differing key oceanographic characteristics at specific times of the year (Egevang et al., 2010; Shaffer et al., 2006). Temperature-depth recorders reveal that seabirds may dive to extreme depths to secure prey, like the Kerguelen Shag *Phalacrocorax verrucosus* (~150 m) (Cook et al., 2013) or that they may prey at the thermocline, which concentrates prey at certain depths (Pelletier et al., 2012). The intersection of tracking and bathymetry data enables determining whether birds are feeding near the seafloor or in the water column, thus providing information about prey behaviour itself (Cook et al., 2012). Additionally, oesophageal temperature loggers or HALL sensors inform not only on the depth at which the prey is ingested, but also on its size (Charrassin et al., 2001; Wilson et al., 2002).

The parallel development of stable isotope and fatty acid analyses (Karnovsky et al., 2012) is shedding light on seabird diet and foraging areas outside of the breeding season (Cherel et al., 2000) and on centennial level regime shifts in the ecosystem, and how these affect seabird population dynamics (Becker and Beissinger, 2006). Currently, our knowledge is biased towards processes occurring during the breeding season, as this is when dietary samples can be collected in colonies and activity recorders deployed on birds. Future research should focus on the life cycle as a whole, integrating the adult breeding and wintering periods (Thiebot et al., 2011), and the juvenile and immature phases (Sherley et al., 2013).

3.4.2. Large teleost fishes

Predatory fishes can provide valuable information about the food web when compared over space and time. For example, tropical tunas are opportunistic, non-selective predators due to their high energy requirements in oligotrophic habitats. Comparative diet studies of yellowfin tuna (*Thunnus albacares*) have provided evidence of spatial and temporal variability in forage species distributions (Olson et al., 2014) and in ecological relationships within the food web. In particular, Olson et al. (2014) found evidence for dramatic decadal-scale changes in the prey of yellowfin tuna in the eastern tropical Pacific, from epipelagic fishes in the early 1990s to mesopelagic fishes and a crustacean in the early 2000s. Pacific-wide comparisons are beginning to link prey diversity to oceanic productivity (Young and Olson, unpublished data). For some other species, such as the albacore and bluefin (*Thunnus thynnus*) tunas, data suggest selection towards prey with high caloric content and/or abundance (Goñi et al. 2011; Logan et al. 2011). Moreover, in the case of albacore tuna, feeding strategies vary geographically (between shelf break and offshore as well as between tropical and temperate latitudes), as well as between day and night (Goñi et al., unpublished data; Williams et al., 2015). Similar patterns have been observed for southern bluefin tuna (*Thunnus maccoyii*) off southeastern Australia (Young et al., 1997), where sub-adults fed in more productive inshore waters and then returned offshore to warmer waters in the East Australian Current, possibly as a thermoregulatory response (Gunn and Young, 2000).

For pelagic fish predators off eastern Australia, when prey composition, prey length, predator depth distributions and feeding times were all taken into account, each predator was in some way distinguished from the others, indicating niche segregation in species that overlap spatially (Young et al., 2010). Whether these patterns are consistent across oceans is the focus of a major review presently underway (Olson et al., unpublished).

3.4.3. Marine mammals

Foraging tactics, prey base and energetic requirements among marine mammal guilds are highly diverse (Reynolds and Rommel, 1999). Historically, the majority of diet information for marine mammals have come from stranded individuals, stable isotope analysis or scat in the case of pinnipeds (Deagle and Tollit, 2007; Hobson et al., 1996; Pauly et al., 1998). The bulk of estimates of forage resources consumed by marine mammals come from the subarctic, with population level estimates of up to 2.3 trillion kj yr^{-1} for fur seals, but data gaps make generalisations across guilds impossible (Hunt et al., 2000). Research on fatty acids and amino-acid specific stable isotopes of blood and tissues offers the ability to further discriminate among prey types at multiple temporal scales (Budge et al., 2006; Schmidt et al., 2004). Mixing models based on $\delta^{13}C$ and $\delta^{15}N$ values of skin and blubber compared with

known prey values are proving useful in determining prey composition, particularly given the cryptic nature of many marine mammals (Kiszka et al. 2014).

One of the most important tools for understanding mammal trophodynamics has been telemetry technology. For pinnipeds, archival tags that are deployed and retrieved at breeding grounds can be used to measure distribution, foraging effort via movement models and more recently even energetic gain as a function of drift rate (Fauchald and Tveraa, 2003; Schmidt et al., 2004; Tremblay et al., 2007). Area-restricted search behaviours have been identified for baleen whales equipped with satellite tags, identifying important migratory corridors and foraging hotspots for blue whales in the Pacific (Bailey et al., 2009). Fine-scale short-duration tags have been critical in matching prey resources to foraging behaviour on appropriate time and space scales. Tags of this type have provided the first direct foraging measurements for deep-diving odontocetes based on foraging clicks, capture events, and more recently size estimates of their individual prey items (Johnson et al., 2004; Madsen et al., 2007). Fisheries echosounders have offered the ability to measure the prey-scape for these toothed whales foraging on the deep scattering layer (Benoit-Bird and Au, 2003; Hazen et al., 2011). Details on consumption and broader prey capture rates have been estimated, but more work is needed to understand the detailed foraging requirements of the wide diversity of marine mammals.

3.4.4. Sharks

Sharks are apex predators in most marine communities, often playing an important role in controlling community dynamics through top-down regulation of prey (Baum and Worm, 2009). Despite their important contribution to the structure and function of an ecosystem, information on their trophic ecology is scarce, largely due to logistical difficulties and conservation concerns associated with their sampling. Many existing ecosystem models still lump sharks into very broad and generic categories, although they are known to display a range of prey capture methods (ramming, biting, ambush, suction, scavenging and filter feeding) and have broad feeding strategies (generalists to specialists) (Wetherbee et al., 2004). This has spurred a recent increase in the number of trophic studies undertaken on oceanic and pelagic sharks, mostly facilitated by advances in new methodologies.

Acoustic telemetry techniques, such as pop-up satellite archival tags, are increasingly used to explore horizontal and vertical movement patterns of sharks, detailing key trophic information such as the identification of their essential foraging grounds (Kock et al., 2013). Biochemical tracer techniques such as bulk stable isotope analysis (Shiffman et al., 2012) and signature fatty acid analysis (Pethybridge et al., 2011) are allowing time-integrated dietary signatures to be acquired based on minimal numbers of specimens. Such studies are demonstrating that sharks have more complex trophic interactions than are accounted for in existing ecosystem models. Using these combined techniques, McMeans et al. (2013) demonstrated that the Greenland shark (*Somniosus microcephalus*) specialised their predation on marine mammal blubber, and that there were substantial prey composition differences between geographically separated populations. The combination of both tracking and various biochemical methods is likely to give greater insight into the feeding ecology of sharks.

4. Trophic hotspots: critical regions for diversity and biomass

Marine "hotspots" are areas in the ocean with either (a) high biodiversity, (b) high concentration of a population or life history stage or (c) high ecological functioning such as trophic transfer. Hotspots often have high conservation need (Hazen et al., 2013)

and are critical for understanding top predator ecology and migration, and the effect of climate change on marine biodiversity. For example, the Global Ocean Biodiversity Initiative (GOBI) has defined 7 criteria for designating Ecologically and Biologically Significant Areas (EBSAs). Here we focus on two of the ecological criteria: areas with high biological production and high biological diversity (Dunn et al., 2011). Identifying hotspot locations is critical, but more importantly we need to understand the mechanisms of formation and persistence that result in high prey availability to top predators. These mechanisms can include interactions with topographic or bathymetric features (Croll et al., 2005; Dower and Brodeur, 2004; Johnson et al., 2004; Morato et al., 2010), but also mixing of ocean water masses and shear from ocean currents (Doniol-Valcroze et al., 2007; Kappes et al., 2010; Polovina et al., 2001), or both (Davoren, 2013). Mesoscale features (e.g. filaments or eddies) or sub-mesoscale features (Lévy et al., 2012) are often nested in broad-scale features, such as where cool nutrient rich waters meet oligotrophic waters in the transition zone of the north Pacific (Block et al., 2011; Polovina et al., 2001), or in eastern boundary upwelling systems (Gruber et al., 2011). Bathymetric hotspots are likely to be more resistant to climate shifts than areas where water masses mix, while there is much debate about how upwelling dynamics will change in eastern boundary currents (Bakun, 1990; Gruber et al., 2012; Harley et al., 2006; Snyder et al., 2003).

Mechanistically, trophic hotspots can result from bottom-up forcing from nutrients to top predators or can result from the aggregation of mid-trophic prey. For example, bottom-up processes, such as upwelling of nutrients, leads to phytoplankton blooms at a week or two lag, followed in a few months by aggregations of mid-trophic organisms, and ultimately top predators once the mid-trophics are at sufficient densities (Croll et al., 2005). Similarly, upwelling areas where productive waters are retained close to shore (such as northern Monterey Bay and the Gulf of Ulloa off Baja California) support a bottom-up food-web that provides foraging habitat for top predators (Graham and Largier, 1997; Wingfield et al., 2011). Fine and mesoscale features such as convergent fronts or eddies can result in shear zones between different water masses or current flow speeds that serve to bio-accumulate prey species (Menkes et al., 2002), and this process can result in hotspot formation and dissipation faster than bottom-up processes (Prairie et al., 2012).

The strength of these hotspots can be a function of the amount of nutrients transported into the photic zone, but also dynamics of the hotspot that increase availability of prey to ocean food webs. Both the persistence and recurrence of these hotspots are critical in evaluating their overall importance to top predators. Very little research has examined scales of persistence and recurrence, but (Suryan et al., 2012) have identified remotely-sensed chlorophyll persistence metrics that underlie seabird hotspots in the California current. Biodiversity hotspots have shifted across the planet at geological time scales, and climate change is likely to only speed up the process in the future due to the dynamic nature of marine systems (Renema et al., 2008; Sunday et al., 2012). Research on the mechanistic links that result in trophic hotspots will certainly aid our ecological understanding but will also help guide the preemptive management strategies best suited to protect pelagic habitat into the future.

4.1. The role of seamounts and static bathymetric features

Hotspots that are temporally and spatially predictable can occur around bathymetric features, such as shelf breaks, canyons and seamounts. These features typically alter the water flow above them, increasing vertical nutrient flux and material retention that support highly productive plankton blooms or swarms (M.R. Clark

et al., 2010; Hyrenbach et al., 2000), and affect the distributions of micronekton (De Forest and Drazen, 2009). The unique "magnetic signatures" of most seamounts also appear influential in attracting migratory species that use them to rest and feed (Morato et al., 2009). Turbulent water flow in the lee of emergent seamounts also serves to retain the planktonic food sources of pelagic fish (Rissik and Suthers, 2000). These features have been shown to act as highly effective natural aggregation mechanisms for tuna and other migratory species, primarily for feeding (Holland and Grubbs, 2007; Hyrenbach et al., 2002; Morato et al., 2008; Young et al. 2011) but also for resting or breeding (Hearn et al., 2010). Seabirds in particular appear drawn to feeding grounds around seamounts (Amorim et al., 2009; Hyrenbach et al., 2002), although some marine mammals, such as monk seals, also utilise prey specific to seamounts (Parrish, 2009).

Existing research has shown increased abundance of the larvae of some tuna and billfish species near oceanic reefs and islands (Fowler et al., 2008). A further study has indicated that broadbill swordfish have resident populations in the vicinity of seamounts (Speare, 2003). The attraction to seamounts is likely to be species-specific; for instance, Morato et al. (2010) found that among the species they examined in the Western Pacific Ocean, porbeagle sharks (*Lamna nasus*), short-finned mako sharks (*Isurus oxyrinchus*), silky sharks (*Carcharhinus falciformis*), yellowfin tuna, blue marlin (*Makaira nigricans*), and swordfish (*Xiphias gladius*) aggregated around seamounts. Sophisticated remote sensing tools can map the position, movement and extent of areas likely to attract aggregations of pelagic life (Game et al., 2009). Protecting static habitats that support high densities of predators will be easier than protecting temporally and spatially dynamic hydrographic features (Morato et al., 2010).

4.2. The role of upwelling in eastern boundary currents

Upwelling ecosystems are typically characterised by a high productivity and endemicity, a dominant biomass of small planktivorous pelagic fishes and strong inter-annual variability in fish recruitment (Checkley et al., 2009). Small pelagic fishes can exert 'wasp-waist' control on their prey and predator species (Cury et al., 2000). Top predators dependent on these small pelagic fishes are, therefore, strongly impacted by fluctuation in their numbers; for example, numbers of breeding endemic seabirds in the Benguela upwelling fluctuate from year to year in relation to the biomass of prey available in the system (Crawford and Jahncke, 1999). Being driven by climatic and oceanographic processes, upwelling systems, especially when they are overfished (Hobday et al., 2015), are expected to be particularly vulnerable to climatic shifts, although there are divergent views on responses. A common view is that, while offshore waters warm up (increasing stratification and lowering primary productivity), inshore regions will experience stronger upwelling due to increased wind-stress (lowering water temperature and increasing primary productivity). An opposing view is that the trade wind system which drives upwelling-favourable winds will weaken with ocean warming, leading to lowered upwelling in inshore waters (Checkley et al., 2009).

5. Climate impacts on trophodynamics and top order predators

Throughout this review we have provided many examples of how climate change will impact the trophodynamics of marine top predators. A range of issues are common across many of the trophic groupings (Box 1).

Climate change may act directly on the physiology, behaviour and survival of top predators, or indirectly, though impacts on the ecology and behaviour of their prey or lower foodweb groups. An example of potential complex trophic interactions is the large scale expansion of the oxygen minimum zone (OMZ) in the tropical and subtropical oceans (Stramma et al., 2008; Stramma et al., 2010). For tunas and billfishes, biological consequences of an expanding OMZ include habitat compression, which can have profound implications (Prince and Goodyear, 2006; Stramma et al., 2011). Shoaling of the OMZ restricts the depth distribution of these and other pelagic fishes into a narrower surface layer, compressing their foraging habitat and altering forage communities. Enhanced foraging opportunities for all epipelagic predators could alter trophic pathways and affect prey species composition. In addition, with a shoaled OMZ, mesopelagic vertically-migrating prey, such as phosichthyid (i.e. *Vinciguerria lucetia*) and myctophid fishes and ommastrephid squids, would likely occur at shallower daytime depths and become more vulnerable to epipelagic predators (Stramma et al., 2010). These are among the taxa that increased most in the yellowfin diet in the eastern tropical Pacific between the 1992–1994 and 2003–2005 sampling periods (Olson et al. 2014).

Studies in the Benguela upwelling system provide another example of the potential complexity of climate change effects through interaction with other factors (Checkley et al., 2009). In the northern Benguela, populations of sardines (*Sardinops sagax*) and anchovies (*Engraulis encrasicolus*) have remained collapsed since their overexploitation, 45 years ago (Griffiths et al., 2004), threatening species of top predators, such as the community of seabirds specialised on small pelagic fishes (Crawford, 2007). Environmental anomalies involving unusual low oxygen events are thought to have prevented the return of small pelagics (Cury and Shannon, 2004). This combination of overfishing and environmental forcing has shifted the system towards a regime dominated by jellyfish and their predator the bearded goby (*Sufflogobius bibarbatus*) (Utne-Palm et al., 2010). Although the goby has become the staple food of seabirds, it has not filled the niche

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Box 1–Summary of major climate change effects and impacts on the trophodynamics of marine predators.

Climate change effects	Impacts and vulnerabilities to trophodynamics
• Ocean acidification • Temperature rise • Shoaling of mixed layer depth, oxygen minimum zones • Circulation changes (e.g. ENSO) • Biogeochemical feedback processes • Sea level rise	• Alterations to food chain length and complexity (energy transfer efficiency) • Decreased productivity • Biodiversity hotspots • Shifts and restrictions in population abundances and distributions • Alterations in species assemblages (food availability to higher order predators)

previously occupied by small pelagic fishes in terms of biomass. Furthermore, its energy content is only half that of sardine and anchovy (Ludynia et al., 2010). In other words, seabirds must consume twice as much of a resource which is not nearly as abundant, meaning a considerable increase in foraging expenditure. In the southern Benguela, anchovy remained available in the system after the sardine fishery collapsed. Sardine has even been gradually returning since the mid-1980s (Griffiths et al., 2004). The benefits, in terms of fish mass, of catching one sardine outweigh the benefits of catching one anchovy by a factor of seven (Fairweather et al., 2006; Funamoto and Aoki, 2002; Van der Elst, 1993), potentially decreasing seabird catch per unit effort. However, the geographical distribution of sardine has shifted eastward since 1996, possibly as a result of climate change in conjunction with the influence of the strong fishing pressure to the West of Cape Agulhas (Coetzee et al., 2008). The sea surface temperature of the inner shelf zone to the East of Cape Agulhas is colder than before, resulting from an increase in wind-induced coastal upwelling linked to a change in zonal wind-stress forcing (Roy et al., 2007). Birds are now declining at their traditional breeding grounds while potential new breeding sites (islands) are lacking along the coastline where resources have become more abundant.

Complex cumulative effects are also expected related to ocean acidification. Carbonate under-saturation resulting from increased ocean CO_2 uptake is expected to directly impact organisms that utilise hard carbonate body structures (Fabry et al., 2008; Orr et al., 2005). However, acidification has also been shown to influence the physiology of a wide range of marine organisms through acid-base imbalance and reduced oxygen transport capacity (Fabry et al., 2008). A cumulative effect with decreased oxygen levels and ocean warming can therefore be expected. The impacts of acidification are predicted to be felt in the California Current upwelling system and the Southern Ocean in the coming decades (Gruber et al., 2012; McNeil and Matear, 2008). Differential responses of species to these and the other changes mentioned above, highlight the need for a detailed knowledge of the trophic ecology of top predators, and the dynamics of the food webs of which they are a part, in order to understand climatic and anthropogenic ecosystem impacts.

6. Model development

The target for much of the trophodynamics research is the development of realistic ecosystem models, as they provide theoretical frameworks in which to assess the ecological impacts of fishing and other perturbations, allowing more strategic and sustainable management. Over the last century, advances in computational power and numerical techniques have assisted the establishment of a number of ecosystem modelling platforms, including: end-to-end and dynamic system models [e.g. Ecopath with Ecosim/Ecospace (Polovina and Ow, 1985; Walters et al., 1999), ATLANTIS (Fulton et al., 2004), SEAPODYM (Lehodey et al., 2003), and various biogeochemical models], individual based models [e.g. OSMOS (Shin and Cury, 2001)], bioenergetics and allometric models (Maury and Poggiale, 2013), and simpler traditional predator–prey models. Although each model operates using different criteria (e.g. level of complexity and realisms, and formulation of functional responses), most are based on the concept of network budget analysis of energy, carbon or mass flow and thus, rely on a thorough understanding of prey-predator relationships.

Despite considerable advances and management reliance, the ability of most ecosystem models to accurately quantify and project responses to stressors, particularly fisheries and environmental changes, is currently limited by large uncertainties in the empirical data used to parameterise models and assess their performance. Some would argue that ecosystem models are rarely quantitative and that purely qualitative models may provide a more realistic approach (Dambacher et al., 2010). Other significant challenges include dealing with multiple biological processes that operate over different scales and interact with different physical and chemical processes (Evans et al., 2013). Current ecosystem models are attempting to overcome such issues, including running dynamic simulations at global scales (e.g. SEAPODYM and NEMURO models), utilisation of multiple ecosystem models, and incorporating data derived from the analyses of bulk stable isotopes (Navarro et al., 2011) and signature fatty acids (Perhar et al., 2013). Bayesian hierarchical modelling frameworks and stochastic process models are assisting parameter estimation and state forecasting (Parslow et al., 2013), while greater inclusion of allometric scaling and ecophysiological properties, based on the dynamic energy budget theory, are enabling greater scale (individual to ecosystem, seconds to decade) integration (Maury and Poggiale, 2013). Consideration of uncertainty in model structure, parameter estimates and data remains an aspect of ecosystem models that has lagged behind other aspects of model development (Evans et al., 2015).

7. Future directions

Adequately assessing the trophic status of large, complex and highly dynamic ecosystems has proved challenging to marine scientists. Future research (Box 2) will need to include strategies for inter-ocean collaboration (e.g. Dambacher et al., 2010) and data sharing built around operational guidelines now commonplace within oceanographic communities. Long-term monitoring (Nicol et al., 2013), increased reliance on biochemical techniques (Pethybridge et al., 2013) and the inclusion of feeding information from archival and associated tags (Bestley et al., 2008) will all increase the broader understanding of top predator trophodynamics. Statistical techniques, such as those using classification trees (Kuhnert et al., 2012) are showing great promise in bringing disparate data sets together. Improvements to the parameterisation of ecosystem models, in addition to the inclusion of more physiological-based (mechanistic) principals, are key priority areas in achieving ecosystem-based management practices.

This review has highlighted the diverse literature on the subject, and we must acknowledge that we have only cited a relatively small portion of the research to date. A major reason for this is that most of this type of research is regionally based. Broad-scale studies are less common and are largely left to modelling studies. However, there is potentially a much greater understanding that can be gained from comparative studies within and across ocean basins. Understanding the dynamics of marine hotspots is important for understanding the trophic ecologies of species and optimising conservation efforts in the future.

Long-term studies are also rare. Convincing funding agencies of the need to include trophic monitoring in long-term time series is a challenge (Nicol et al., 2013). Long-term observation will allow us to examine and understand the effects of climate variability on the ecosystem to ultimately obtain more mechanistic and realistic models for improved prediction by incorporating observed changes in the ecosystem, e.g. dietary shifts.

Numerous data gaps remain in our understanding of micronekton, including their composition, drivers of their trophodynamics, and the contribution of the gelatinous component. These data gaps exist in part because of the mesopelagic distributions of many micronekton species, and the difficulty in sampling them. Coupled with improved knowledge of micronekton, more detailed

Box 2–Key research gaps and related priorities.

Research Gaps	Priorities
Trophodynamics of some trophic groups	Undertake more research on micronekton assemblages, gelatinous zooplankton, non-harvested intermediate species (of cephalopods, small pelagic fishes) and sharks.
Long-term observations	Implementation of monitoring stations in biodiversity 'hotspots'.
International collaboration	Large, basin-scaled comparative studies. The establishment of international working groups such as those through IMBER are assisting, but greater collaboration is needed.
Interdisciplinary	Focus on the interactions and linkages between biogeochemical cycles and food webs. Dual methods approaches will also be useful in obtaining more data.
Early life history feeding	Application of biochemical techniques that are already being utilised for other life stages or taxa.
Ecosystem model data uncertainty	Better usage of data derived from biochemical tracers and tagging, including a need to standardise related statistical approaches. This could involve potentially modifying ecosystem models to represent such biochemical data.
Mechanistic understanding of key environmental and biological (e.g. physiological and evolutionary) drivers of trophic groups	Establish quantitative relationships between short-term, small-scale processes (e.g. individual movement behaviors and physiological constraints), and their long-term, large-scale population level effects. Data mining, including the utilisation of existing biological, biochemical, oceanographic data should help identify patterns.
Impact of climate change on marine trophodynamics	Monitoring of key trophic species within hotspot and climate sensitive areas. The implications of anthropogenic driven increases in gelatinous organisms to the ecology of top predators needs further exploration.

information is required on the diets of top predators, to better distinguish between species interactions and the potential for top down food web effects. The range of top predator interactions in ecosystem models also needs to be expanded beyond the large fishes and more consistently include other predators such as marine mammals, seabirds and turtles, and explicitly focus on how they partition resources in both space and time.

Potential future directions for trophodynamic research on early life stages are plentiful. They range from simply expanding our basic knowledge of the taxa we know nothing about, to the application of existing biochemical techniques. The challenges of studying the larvae and juveniles of large pelagic species are numerous, and the greatest hurdle may be the substantial amount of resources needed to adequately sample the taxa that inhabit entire ocean basins, or are distributed unevenly and unpredictably. Trophodynamic studies on the early life stages of top predator species often provide only isolated snapshots because of the vastness in both space and time over which the larvae and juveniles occur. While informative, these studies usually fail to provide a sense of how prevalent the observed diets or indices of feeding success are for the wider population.

There is also a need to go beyond simple observations, relating what we learn about trophic interactions to larger-scale processes such as growth (Jenkins et al., 1991), fishing pressure (Williams et al., 2015), survival and the mechanisms influencing prey availability (Olson et al., 2014). Such information will enhance our ability to understand how climate change, fishing, and other stressors might impact survival and, thus, top predator populations as a whole. By combining traditional dietary sampling techniques with activity recorders and biochemical methods, we are developing a 'super-tool' for describing the relationship between predators and their prey at different levels of space and time, something which is crucial for guiding conservation and sustainable management measures for top predators.

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