

Coastal marine ecosystem connectivity: pelagic ocean to kelp forest subsidies

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Abstract. The movement of trophic resources between and among ecosystems, referred to as cross-ecosystem subsidies, is a common phenomenon. In the marine environment, both adjacent and distant ecosystems are connected by oceanographic forces that transport nutrients, organisms, and other materials. Kelp forest ecosystems are one example of an open marine system that both exports and receives trophic subsidies. Though rocky reefs are rich in kelp-based energy produced internally, kelp forest organisms also rely on phytoplankton, and the influx of holoplankton and meroplankton from adjacent open ocean habitats. In this paper, we seek to clarify the identity of holoplanktonic and meroplanktonic subsidies, quantify their energetic and nutrient contributions to the kelp forest, and further explore the impacts of these subsidies for individual consumers and for kelp forest communities. We reviewed six individual subsidy organisms that are commonly advected to kelp forests on the West coast of North America, and show that these organisms from the pelagic ocean represent important resource pulses for kelp forest consumers. In addition, we summarize the characteristics of subsidies, consumers, and recipient ecosystems that provide insight into the dynamics of subsidy influx and impacts to recipient systems. Finally, we provide suggestions as scientists move forward with efforts to quantify the impacts of cross-ecosystem subsidies. Trophic subsidies are a major force shaping both marine and terrestrial communities and ecosystems. Quantitative information about these subsidies and their impacts on food webs will not only improve our understanding of these ecosystems, but also improve food web models, and predictions of ecosystem response to change.

Key words: allochthonous inputs; coastal ecosystems; ecosystem connectivity; kelp forest; pelagic-benthic coupling; trophic subsidy.

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INTRODUCTION

Cross-ecosystem subsidies and the movement of animals from one ecosystem to another play a fundamental role in the trophic structure of communities and the dynamics of food webs (Polis et al. 1997, Palumbi 2003, Marczak et al. 2007). While ecosystem connectivity is the rule in natural systems, not the exception, we are far from fully understanding the food web impacts of

energy and nutrients that come from other ecosystems. Often termed trophic subsidies, these are donor-controlled resources (i.e., a resource with dynamics determined outside of the recipient system) that originate in one ecosystem but are moved to another (Polis et al. 1997). A subsidized system can be defined as a geographic area whose boundaries do not encompass the entire area of production that supports it (Trebilco et al. 2016). In terrestrial systems,

subsidies occur predominately via rivers (Sabo and Power 2002, Power et al. 2004, Richardson et al. 2010), the movement of animals that transport and deposit nutrients derived in one ecosystem to another (e.g., birds and bats depositing guano: Anderson and Polis 1999), and animal migrations (migration-mediated subsidies: Bauer and Hoyer 2014; subsidies related to fish migrations: Flecker et al. 2010). Salmon and other anadromous fishes link highly productive oceans with upstream watersheds (Garman and Macko 1998, Cederholm et al. 1999, Naiman et al. 2002, Moore et al. 2007). Seabirds deposit marine-derived nutrients on rocky islands and surrounding ecosystems in the form of guano, providing an influx of nitrogen and phosphorus to recipient ecosystems (Anderson and Polis 1999, Maron et al. 2006, Honig and Mahoney 2016). Carbon and nitrogen derived from riparian plants and mangroves fuel aquatic food webs below (Nakano and Murakami 2001, Wallace et al. 2015, Yeager et al. 2016). Marine macrophyte detritus creates habitat and energetic resources for detritivores, consumers, and predators both in supralittoral beaches (Orr et al. 2005, Dugan and Hubbard 2016, Liebowitz et al. 2016) and in the subtidal benthos (Vetter 1994, Vetter and Dayton 1998, Britton-Simmons et al. 2012).

Marine trophic subsidies are ubiquitous throughout the ocean environment (Willson and Womble 2006). There is a long history of studies describing these subsidies and their impacts in terrestrial and freshwater systems, but the exploration of subsidies within and among marine ecosystems is relatively new (Gaines and Roughgarden 1985, Bustamente et al. 1995, Willson and Womble 2006, Krenz et al. 2011, Filbee-Dexter and Scheibling 2016, Henschke et al. 2016, Griffiths et al. 2017, Morgan et al. 2018). This is despite the fact that in marine ecosystems, genetic material, larval and juvenile organisms, nutrients, and habitat structure move between and among ecosystems on scales that are uncommon in terrestrial counterparts. Indeed, marine systems are considered more open than terrestrial systems (Carr et al. 2003). This basic feature of the marine environment suggests that subsidies are likely quite prevalent and that subsidies from the pelagic ocean have the potential to be widely consumed by the numerous planktivorous species present in nearshore environments

(Carr et al. 2003). The rain of phytoplankton, zooplankton, fecal pellets, and detritus (often referred to as marine snow) delivers energy to deep-sea habitats (Iseki 1981, Stockton and DeLaca 1982, Alldredge and Silver 1988, Britton-Simmons et al. 2012, McClain et al. 2018); forage fish such as menhaden undergo migrations from rearing estuaries to nearshore coastal areas, exporting large magnitudes of carbon, nitrogen, and phosphorus to the marine system (Deegan 1993); and nutrients from rivers are exported to nearshore food webs (Foley and Koch 2010, Richardson and Sato 2015). These marine spatial subsidies can represent sustained and continuous nutrient and energy delivery (as in the case of marine snow to deep-sea habitats), or pulses of prey lasting for short periods, with wide-ranging implications for consumer responses (Holt 2008). Yet all of these subsidies are donor-controlled, with resource availability, timing, and magnitude determined by forces outside of the recipient ecosystem (Polis et al. 1997).

The ecological relevance of subsidy flows in the marine environment is highlighted by several especially well-studied examples of cross-ecosystem subsidies. Polis and colleagues combined field surveys and stable isotopes analysis to extensively document individual, community, and ecosystem-wide impacts of marine-based algal wrack and seabird guano on nutrient-poor island desert ecosystems (Polis and Hurd 1996, Anderson and Polis 1998, 1999, Spiller et al. 2010). This research traces terrestrial food web pathways of marine subsidies, finding positive community and population outcomes for terrestrial consumers. Recent experimental manipulations of beach wrack showed that subsidies increase detritivore biomass (amphipods) and predator populations (terrestrial lizards), though the mechanisms for these impacts are still being investigated (Spiller et al. 2010, Wright et al. 2013, Dugan and Hubbard 2016). Norwegian herring migration from oceanic feeding grounds to coastal overwintering and spawning areas represents a massive annual influx of energy used by benthic fish predators and crustaceans (Varpe et al. 2005). Further, investigation into effects of this subsidy on cod (herring predators in the recipient ecosystem) revealed positive impacts on population productivity from this large-scale movement of energy (van Deurs et al.

2016). Experiments with algal detritus in subtidal habitats have shown that macrophyte subsidy piles generate increased abundance of copepods and amphipods; the drift algae act both as a habitat to hide in and as a trophic resource (Vetter 1995, Duggins et al. 2016). Despite these well-described examples, our lack of knowledge of the dynamics of marine subsidies and how these dynamics link to individual- and population-level responses continues to undermine a comprehensive understanding of food web dynamics.

The history of subsidies work in marine systems has, not surprisingly, focused on large inputs of energy to unproductive systems such as sandy beaches (Orr et al. 2005, Netto and Meneghel 2014, Liebowitz et al. 2016), desert island ecosystems (Polis and Hurd 1996, Spiller et al. 2010), and the deep sea, in the form of whale falls (Smith and Baco 2003), or detrital subsidies to deep benthic habitats (Vanderklift and Wernberg 2008, Britton-Simmons et al. 2009, Filbee-Dexter et al. 2018). In these ecosystems with low endogenous productivity, the effect of subsidies on consumer–resource dynamics is often more evident, with recent studies finding the strongest consumer responses to subsidies in recipient habitats with low productivity (Sabo and Power 2002). Similarly, there are examples of subsidies that provide a particular limiting nutrient to systems that might otherwise support high rates of primary and secondary productivity. Phosphorus is limiting in certain mangrove and coastal nearshore systems, but cross-system subsidies provide this nutrient with follow-on ecosystem impacts (mangroves: Adame et al. 2015; nearshore coastal environments: Deegan 1993). Lacking, however, are studies looking at the extent and impact of cross-ecosystem trophic subsidies to systems that are known for their high internal productivity.

Kelp forests in temperate coastal oceans are one of the most productive ecosystems in the world (Schiel and Foster 2015). Though literature about kelp forest subsidies exists, the majority focuses on kelp forests as a source rather than a recipient ecosystem (Bustamente et al. 1995, Vetter and Dayton 1998, Dugan et al. 2003, Rodríguez 2003, but see Docmac et al. 2017). However, the diversity of planktivores (e.g., filter-feeding invertebrates) in kelp forest

ecosystems that have evolved to take advantage of the constant stream of plankton being delivered to the forest highlights the role that subsidies play in kelp forest community organization. Indeed, kelp forests are the recipients of trophic subsidies from a variety of sources, from adjacent rivers to the pelagic ocean (Bray et al. 1981, Foley and Koch 2010, Docmac et al. 2017, Galloway et al. 2017). These sustained or short-term pulses of energy can be predictable or sporadic, but undoubtedly have consequences for predators, trophic interactions, and community composition.

The primary productivity that fuels the diversity and abundance typical of a kelp forest comes from two sources. Endogenous productivity of macrophytes (predominately kelps, but also green and red algae, and seagrasses) and energy derived from phytoplankton both within and outside of the kelp forest both contribute to the growth and survival of kelp forest organisms (Duggins et al. 1989, Schiel and Foster 2015). Though several studies have addressed the relative importance of these two autotrophic groups to kelp forests (the nutritional value of kelp-derived material for organisms in nearshore food webs is an active area of research), we know substantially less about the importance of phytoplankton and exogenous subsidies fueled by phytoplankton (Duggins and Eckman 1997, Graham 2004, Miller et al. 2011, Dethier et al. 2014, Koenigs et al. 2015). The most comprehensive efforts estimate that the production of giant kelp (*Macrocystis pyrifera*), the predominant macroalgae in central and southern California kelp forests, is approximately $5.5 \text{ kg}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Rassweiler et al. 2018). Although robust estimates of phytoplankton production within kelp forests and influx to kelp forests are not available, research suggests that coastal macrophyte production may be five to ten times greater than phytoplankton production (Kavanaugh et al. 2009, Schiel and Foster 2015). Since phytoplankton and macroalgal productivity exhibit spatial variation on both local and broad coastal scales (Broitman and Kinlan 2006, Kavanaugh et al. 2009, Fiechter et al. 2018), the relative importance of macroalgae or phytoplankton production in a kelp forest likely varies in space, seasonally and annually, and along shorelines (Duggins et al. 1989, Von Biela et al. 2016). On top of this inherent

variation are changing ocean conditions. Kelp forests along portions of the California coast are currently experiencing a large-scale shift from macroalgae-dominated systems to urchin barrens with little kelp cover, with an accompanying decline in local, kelp-derived productivity (Filbee-Dexter and Scheibling 2016; M. H. Carr, *personal communications*). Phytoplankton-based productivity and the delivery of trophic subsidies could become increasingly important in coming years.

In addition to primary production via phytoplankton, there are episodic influxes of organisms that feed on phytoplankton-based food webs from the pelagic ocean. These trophic subsidies to the nearshore kelp forest are the topic of this review and can be divided into two categories (Menge et al. 2015, Morgan et al. 2018): meroplanktonic organisms where recruiting larvae or juveniles can be considered a subsidy, and holoplanktonic organisms (zooplankton members of the pelagic community) that are transported to the nearshore from the open ocean, typically on ocean currents and internal waves

(Shanks and Wright 1987, Carr and Syms 2006; Fig. 1). These trophic subsidies are not autotrophs but are one to several trophic levels higher. As such, their energy influx reflects a larger contribution of primary production (since energy has been lost during trophic transfer to the subsidy organisms). They can be thought of as trophic intermediaries that deliver phytoplankton-based energy from the pelagic ocean to kelp forest habitats. Although specific examples of these subsidies have been documented, for almost all cases, little is known about the factors that drive variability in subsidy timing, delivery, frequency and magnitude, or their ecosystem and population-wide impacts. Recent research has highlighted the role of small-scale surf zone hydrodynamics in determining the delivery of subsidies to the intertidal zone, and similar oceanographic dynamics likely play a role in subsidy delivery to kelp forests (Shanks et al. 2017, Shanks and Morgan 2018). Though it is unlikely that each individual species representing a trophic subsidy is important to the productivity of kelp forests (relative to in situ

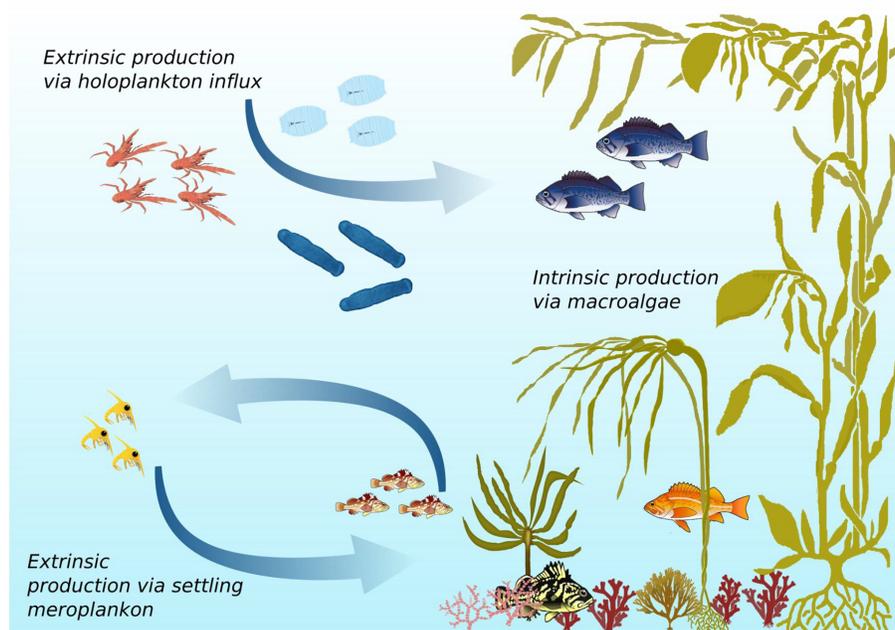


Fig. 1. In addition to the primary production of phytoplankton, there are more episodic influxes energy and nutrients from the pelagic ocean. These trophic subsidies to the nearshore kelp forest can be divided into two categories: (1) holoplanktonic organisms transported to the kelp forest; and (2) meroplanktonic organisms settling to the kelp forest.

macroalgal production), the diversity and number of these species suggests that together, their energy inputs might be quite influential.

Here, we provide an integrative review on the topic of cross-ecosystem trophic subsidies from the pelagic ocean to kelp forest ecosystems. Using case studies, we highlight instances where these cross-ecosystem subsidies have been more thoroughly documented, and places where additional research would greatly improve our understanding, while emphasizing the diversity of pelagic-kelp forest subsidies that exist. Following recommendations from Richardson and Sato (2015), we provide information on the duration and magnitude of the subsidy, the nutritional value of the subsidy, and any known influences on recipient food webs and ecosystems. There are several approaches to scaling the impact of trophic subsidies to the kelp forest ecosystem. Subsidy inputs can be compared to consumer resource demand, to generation time of consumers, to productivity intrinsic to the recipient or donor ecosystems, or in relation to trophic outputs from the recipient ecosystem (Holt 2008, Yang et al. 2008). Marczak et al. (2007) show that the ratio of the energetic value of subsidy resources to equivalent energy produced within the recipient ecosystem is most related to consumer response. However, because data on resources equivalent to the diverse subsidy contributions are not available for kelp forest ecosystems, we simply present subsidy energy values for the recipient system in the case studies below. Specifically, we address three fundamental questions: (1) What is the general identity of subsidies from the open ocean to the kelp forest and what are the estimated contributions of these subsidies? (2) What do we know about how these subsidies impact kelp forest communities and ecosystem functioning? (3) What can we do to better quantify these subsidies and their impacts?

METHODS

We searched the peer-reviewed literature using the Web of Science search engine (“all years” ending in summer 2017) for information on each of the six example subsidies discussed below. For every relevant paper identified, we looked at citations, and at papers that had cited

the originally identified paper. To be included in the synthesis, the paper and data were required to meet the following qualifications: (1) The study and/or measurements must be about the taxa of interest; and (2) the study and/or measurements must be about the life phase of interest for a particular organism. Whenever possible (several categories of data did not exist for the West coast of North America), only data from the specific location of interest were used.

To explore the energetic contribution of a given subsidy to the kelp forest, the following simple equation was used:

$$E = \rho E_i$$

where E = energy delivered in a subsidy pulse per unit area, ρ = density of the subsidy organism in the kelp forest, and E_i = energy content of an individual subsidy organism. When energy content of an individual organism was not known, it was calculated by multiplying the average mass of an individual of the subsidy species by the energy content per unit mass of that species.

While literature values of gross energy content (kcal/g or kJ/g) were available for some species, energy content was calculated from the protein, lipid, and carbohydrate components of proximate composition analyses for others. The accepted values of 5.5 kcal/g (protein), 9.3 kcal/g (lipid), and 4.1 kcal/g (carbohydrates) were used in the conversion (Smith et al. 1975).

PELAGIC ORGANISMS AS SUBSIDIES TO NEARSHORE ROCKY REEF HABITATS (HOLOPLANKTONIC ORGANISMS)

On the West coast of North America, physical mechanisms including upwelling, internal waves, onshore wind waves, and tides deliver nutrients to nearshore kelp forests from the California Current ecosystem (Shanks 1995). In addition to these nutrients, oceanographic forces move animals from one marine habitat to another. Zooplankters, especially those with limited swimming ability, can be transported on currents, internal waves, and with tides to the nearshore environment (see Fig. 2 for holoplanktonic taxa representing potential kelp forest subsidies and Table 1 for a summary of the oceanographic

Holoplanktonic Taxa		Meroplanktonic Taxa	
	Cnidaria Class: Scyphozoa, Hydrozoa		Cnidaria Class: Anthozoa, Hydrozoa
	Ctenophora		Bryozoa
	Annelida		Annelida Class: Polychaeta, Echiura, Hirudinea
	Mollusca Class: Gastropoda, Cephalopoda		Mollusca Class: Gastropoda, Cephalopoda, Bivalvia, Polyplacophora
	Arthropoda Class: Maxillopoda Malacostraca, Ostracoda, Branchiopoda		Arthropoda Class: Maxillopoda, Malacostraca, Chelicerata
	Echinodermata Class: Crinoidea		Echinodermata Class: Crinoidea, Echinoidea, Asteroidea, Ophiuroidea, Holothuroidea
	Chordata: Class: Thaliacea, Appendicularia, Osteichthyes		Chordata: Class: Osteichthyes

Fig. 2. Taxonomic groups (not an exhaustive list) of the common taxa of holoplanktonic and/or meroplanktonic organisms that may serve as trophic subsidies to nearshore rocky reefs on the West coast of North America. Other phyla that likely comprise subsidies to the kelp forest include Rotifera and Chaetognatha (holoplankton), and Porifera, Rotifera, Nemertea, Chaetognatha, Sipuncula, and Brachiopoda (meroplankton).

forces that transport holoplankton to nearshore environments). While these drifting organisms occasionally strand on beaches, many individuals pass through or are retained in the kelp forest where they become prey for a variety of nearshore predators (Fig. 3). We assume here that the vast majority of pelagic organisms advected to the kelp forest are consumed directly in a relatively short period of time, or enter detrital pathways, rather than surviving for longer periods of time in the nearshore environment or emigrating

back to the pelagic ocean. Three examples of pelagic organisms with distinct life histories and dynamics are detailed below.

Pelagic red crabs (Pleuroncodes planipes)

Pelagic red crabs or langostilla (also known as tuna crabs) are one of approximately 200 species of galatheid crabs. Early life phases of red crabs exist in the plankton, followed by an adult life stage (age 2+) that is primarily benthic but includes migrations to the midwater, and a final

Table 1. Oceanographic forces that influence the dynamics of mero- and holoplanktonic subsidy delivery to the kelp forest.

Oceanographic forces	References
PDO/ENSO	Cowen (1985); Lenarz et al. (1995); Field and Ralston (2005); Carr and Syms (2006); Laidig et al. (2007)
Surface currents and waves	Becker et al. (2007 <i>a, b</i>)
Eddies and jets	Ebert and Russell (1988)
Seasonal upwelling/relaxation	Menge et al. (2003); Broitman et al. (2005); Roughan et al. (2006); Wilson et al. (2008); Laidig (2010); Caselle et al. (2010); Markel (2011)
Coastal fronts	Woodson et al. (2012); Ryan et al. (2014)
Tides	Markel (2011)
Internal waves	Woodson (2018)

entirely benthic adult phase (Boyd 1967, Aurióles-Gamboa 1992). Red crab densities can be extremely high in the pelagic environment and occur with a notoriously patchy distribution (Robinson et al. 2004, Pineda et al. 2016). Patches have been observed to span up to 6 km in near-shore waters of <80 m depth, though efforts to estimate patch size have not been comprehensive (Robinson et al. 2004). Echogram observations document the crabs occurring from surface waters to depths of at least 200 m and support the well-known swarming behavior in this species (Robinson et al. 2004). During El Niño years when red crabs strand in Monterey Bay, expert estimates of kelp forest densities range from 5 to 15 individuals/m³ (Fig. 3a). These swarms become especially conspicuous during annual stranding events to shallow water and intertidal beaches that occur in Bahia Magdalena (Baja California, Mexico) during the spring season (the end of crab's reproductive season), and that occasionally occur in southern and central California (Glynn 1961, Aurióles-Gamboa et al. 1994, McClatchie et al. 2016). Annual stranding is well documented in Mexico, but the species has a wide West coast distribution from Panama to Monterey Bay, California (Longhurst 1967, Pineda et al. 2016). It is accepted that red crabs in their pelagic life phase move with warm water to California during El Niño years, though rarely have abundances or densities been measured in California waters (Table 2). Apart from anecdotal evidence, little is known about the magnitude or

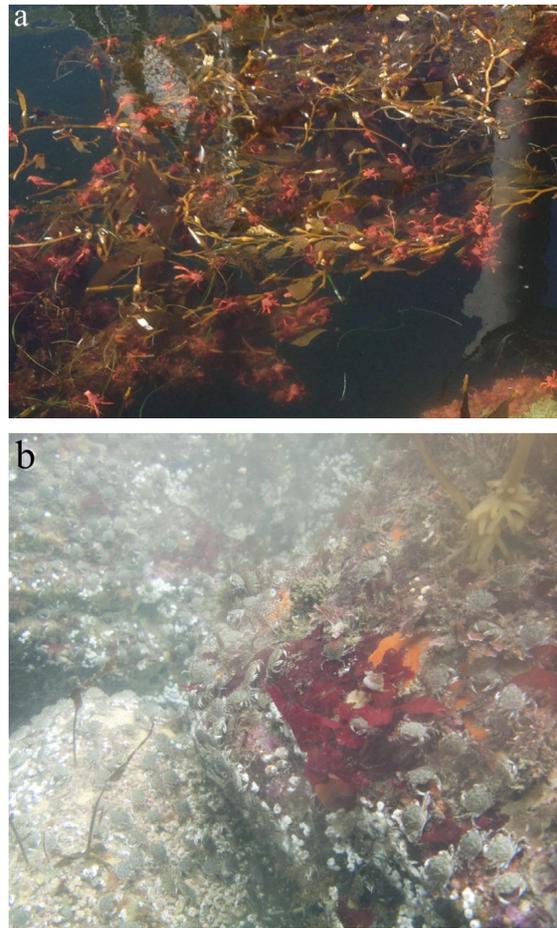


Fig. 3. (a) Pelagic red crabs on kelp (*Macrocystis pyrifera*) in coastal habitats of Monterey Bay, California, in August 2015 (photograph: Rachel Zuercher), and (b) juvenile Dungeness crabs during a recruitment event in Oregon in 2008 (photograph: Scott Groth).

spatial extent of the subsidy in California waters, though we do know that the frequency of occurrence can generally be predicted by El Niño conditions. The specific oceanographic forces that bring red crabs to the kelp forest are not known. Dynamics, however, are quite different in Mexico where the subsidy is annually occurring and spatially predictable.

In the center of their geographic range, pelagic red crabs play an important link between primary production and higher trophic levels, making energy from phytoplankton available to predatory vertebrates and invertebrates (Longhurst 1967, Robinson et al. 2004, Wingfield et al.

Table 2. The occurrence of pelagic red crabs in California (adapted from Lluch-Belda et al. 2005).

Year	Location	References
1859	Monterey Bay, CA	Stimpson (1860)
1895	Monterey Bay	Boyd (1967)
1941	California	Hubbs (1948)
1957–1959	California	Longhurst (1967); Boyd (1967)
1960	Monterey Bay	Glynn (1961); Boyd (1967)
1969	Monterey Bay	Hardwick and Sprat (1979)
1972–1973	Southern California Bight	Stewart et al. (1984)
1978	Ensenada, CA	McLain and Thomas (1983)
1982–1983	California	Lluch-Belda et al. (2005); Stewart et al. (1984)
1984–1985	Monterey Bay	Larson (1991)
1997–1998	California	Lluch-Belda et al. (2005)
2002	California	Lluch-Belda et al. (2005)
2015–2017	California	McClatchie et al. (2016); Sakuma et al. (2016); Connelly (2017); Carr, <i>personal communications</i>

2011). An individual red crab provides an estimated 18.96 kcal (79.33 kJ) to predators (Smith et al. 1975). Using this estimate, we calculate that in nearshore California waters, energy subsidies due to the advection of red crabs from pelagic waters to the kelp forest could reach approximately 1189.95 kJ/m³. Pelagic red crabs are rich in total lipids (e.g., ~14–16% of dry weight), and they are dominated by a nutritionally valuable ω -3 essential fatty acid (20:5 ω 3; 9–21% of total fatty acids; Auriolles-Gamboa et al. 2004).

Pelagic red crabs are not fast swimming, are not camouflaged, and provide a high-energy, high-protein meal. It is not surprising that many organisms prey on pelagic red crabs. The most frequent group of predators observed consuming pelagic red crabs are sea and shore birds. Gulls (*Larus occidentalis*, the western gull, in particular) seem to benefit substantially from the subsidy, both in Baja California, Mexico, where the subsidy is an annual occurrence and in California where pelagic red crabs are sporadic members of the prey assemblage (Stewart et al. 1984, Auriolles-Gamboa et al. 2003). The presence of red crabs during El Niño years (which typically represent low food years for seabirds) was observed to shift roosting patterns in a population of western gulls in California (Stewart et al. 1984). Nearshore rockfish in California also make use of

pelagic red crabs during El Niño years when red crabs are available (Larson 1991). Stomach content analysis paired with analysis of fat reserves led Larson (1991) to conclude that a glut of pelagic red crabs in the nearshore prey assemblage during summer 1984 had effects at the level of individual rockfish physiology. Several species of nearshore rockfish exhibited high levels of fat reserves and high liver weights from summer 1984 to spring 1985.

Pelagic tunicates: salps, doliolids, and pyrosomes (class: Thaliacea)

Together with other gelatinous zooplankton, pelagic tunicates represent a vastly understudied node in marine food webs. Pelagic tunicates refer to members of the class Thaliacea, including salps (family: Salpidae), pyrosomes (genus: Pyrosoma), and doliolids (order: Doliolida). Salps are globally distributed, inhabiting pelagic habitats in all oceans except the Arctic (Lambert 2005). Thaliaceans have both solitary and colonial forms, with colonial organisms reaching up to 20 m in length and solitary forms as small as several centimeters (Lambert 2005). Recent work points to the importance of both salp carcasses and salp fecal pellets as a subsidy to the deep sea, though few researchers have examined salps as a subsidy to the kelp forest (Hobson and Chess 1988, Henschke et al. 2016). While this case study looks specifically at pelagic tunicates, cnidarians and ctenophores represent a similar subsidy to kelp forest systems (though energy densities differ among the taxa).

Limited data exist that quantify the dynamics of pelagic tunicate delivery to nearshore ecosystems. However, in the pelagic environment, gelatinous zooplankton can form swarms that persist for days to months at a time, and certain oceanographic conditions transport these swarms onshore (Hereu et al. 2010, Lucas and Dawson 2014). Several groups have documented a particularly large pyrosome bloom in coastal Oregon and noted that this increased abundance of pyrosomes coincided with increases in salp abundances in their surveys (Brodeur et al. 2018, Sutherland et al. 2018). Extremely high pyrosome densities were encountered during pelagic trawl surveys (over 200,000 kg/km³ off Vancouver Island, Washington), and corresponded with beach strandings of the organisms. Ocean

conditions leading to these swarms are not well understood. Moreover, pyrosomes have been shown to subsidize diverse benthic deep-sea consumers in the NE Pacific when they eventually fall to the bottom (Archer et al. 2018). Smith et al. (2016) show marked temporal variability in the abundance of gelatinous zooplankton (GZ) on the Northeast Atlantic shelf, with periods of high abundance of GZ lasting for approximately five years. In addition, they find a positive correlation between increased abundance of GZ and abundance of benthic scavenging fishes known to consume GZ (Smith et al. 2016).

Our lack of data makes it quite difficult to quantify the trophic importance of pelagic tunicates as a nearshore subsidy, but we can use energy estimates for individual tunicates to begin the process. Energy densities for temperate pelagic tunicates have been estimated at 4.1 kJ/g dry mass (*Salpa* spp.), 5.45 kJ/g dry mass for *Salpa fusiformis*, and 4.94 kJ/g dry mass for *Pyrosoma atlanticum* (Steimle and Terranova 1985, Davenport and Balazs 1991, Clarke et al. 1992, Wang and Jeffs 2014). Because pelagic tunicates are minimally mobile organisms, the vast majority of individuals that are delivered to the kelp forest are either consumed as prey or enter detrital food chains. Using the estimated energy content for *Salpa fusiformis*, an estimated 300 individuals/m³ delivered to the kelp forest (measured in the midwater zone of an Alaskan kelp forest), and an estimated 0.24 g dry mass for an individual salp, energy from the salp subsidy could reach 392 kJ/m³ (Clarke et al. 1992, Pakhomov 2004). Using a 2.0 g dry weight estimate for an individual pyrosome produces an estimate of approximately 9.88 kJ/individual (Davenport and Balazs 1991). Pyrosome lipid profiles are not well studied but are known to be rich in 14:0 and 16:0 saturated fatty acids, 18:1 ω 9 monounsaturated fatty acid, and 20:5 ω 3, 22:5 ω 6 polyunsaturated fatty acids (Davenport and Balazs 1991).

Gelatinous organisms are often considered a trophic dead end in marine ecosystems—organisms unsuitable as prey for most predators, thus unlikely to contribute to the continued flow of carbon up the food chain. Recent work, however, points to widespread importance of gelatinous organisms, including pelagic tunicates, in the diets of many higher trophic species. Though energy content of an individual pelagic salp is

significantly lower than that of a similarly sized fish, pelagic tunicates (and other gelatinous organisms) digest extremely quickly and little energy is expended during digestion or prey capture and handling (Arai et al. 2003). Given the ease of digestion, the occasional very high densities of easily captured tunicate prey have led researchers to question the label of trophic dead-end, especially during tunicate blooms or low abundances of more energy-dense prey. Throughout marine systems, more than 47 species of fish are known to feed on pelagic salps (Kashkina 1986). In the northeastern United States, researchers estimate that spiny dogfish (*Squalus acanthias*) remove 0.3–298 g of gelatinous zooplankters per individual annually, and posit that GZ provides important pulses of food for both spiny dogfish and several species of scavenging fishes (Smith et al. 2016). In California's kelp forests, several species of rockfish are known to consume large quantities of pelagic tunicates when particularly high abundances are present in the kelp forest (Hallacher and Roberts 1985, Hobson et al. 1996). The majority of fishes (and some invertebrates) in nearshore kelp forest systems are generalist feeders, and prey switching to pelagic tunicates in most of these species is relatively unexplored. Pulses of tunicate influx to kelp forests of Carmel Bay, California, USA, during the summers of 2015–2016 led to blue, black, and kelp rockfish (*Sebastes mystinus*, *S. melanops*, and *S. atrovirens*) with stomachs completely full of salps and doliolids, suggesting that these species focus their foraging on this subsidy when densities are high enough (R. Zuercher, unpublished data). During a period of uncharacteristically high salp abundance in the nearshore Alaskan kelp forest, Duggins (1981) observed three to four weeks in early summer where salps comprised approximately 66% of the diet of sea urchins (*Strongylocentrotus franciscanus*, *Strongylocentrotus droebachiensis*, and *Strongylocentrotus purpuratus*).

By-the-wind sailor (Velella velella)

A second gelatinous organism that provides a prominent subsidy to central California kelp forests is the surface-dwelling pelagic hydrozoan, *Velella velella* (hereafter *Velella*). *Velella* have a global distribution in both tropical and temperate open ocean waters and are well known for large-scale beach strandings (Purcell et al. 2015).

Indeed, reports of these large strandings account for much of the data available about *Verella* abundance, density, and movement dynamics. During a documented mass stranding in New Zealand in October–November 2006, a subsidy of approximately 100 million individual *Verella* were delivered to a six-kilometer stretch of beach ecosystem (Flux 2008). For the almost two decades prior to the 2006 New Zealand stranding, only a few individuals per year washed up on the same beaches (Flux 2008). Kemp (1986) documented similar mass strandings on beaches around Newport, Oregon, in 1981 and 1984, with only scattered stranded individuals in 1982, 1983, and 1985. Like pelagic tunicates, *Verella* that are delivered to the nearshore system do not typically return to the pelagic ocean. They are either consumed, enter the detrital food chain, or are stranded where they subsidize coastal beaches. The delivery of *Verella* to the nearshore environment is pulsed, seasonal, and highly variable from year to year. McGwynne (1980) measured beach deposition rates and found highly variable delivery to beaches on the East Cape of South Africa during summer, but essentially zero deposition in the winter. Future research should address the duration of this subsidy and the frequency at which *Verella* are brought to nearshore systems.

Despite the wide distribution of *Verella* throughout tropical and temperate oceans, few have attempted to quantify its importance as a prey item in the kelp forest system. The most comprehensive work was done by Kemp (1986) in coastal Oregon. During strandings in 1984, an estimated 2573 g of ash free dry weight/m of shoreline (1223 g/m carbon, 347 g/m nitrogen) stranded on the beach. During a recent beach stranding in New Zealand, as many as 25,000 individuals/m² were deposited (Flux 2008). As an individual prey item, *Verella* provide approximately 2.9 kJ energy/g dry mass (with an individual *Verella* weighing an average of approximately 0.09 g dry mass) and are likely among the gelatinous organisms that are energetically cheap for predators to capture and digest (Arai et al. 2003, Peckham et al. 2011). To our knowledge, no estimates exist for densities of *Verella* on the surface waters of a kelp forest, and beach densities represent the sum of all *Verella* that moved through the nearshore environment

during a stranding without being consumed. Anecdotal evidence from pelagic waters suggests that it is not uncommon for *Verella* rafts to reach densities of 20 individuals/m². Using this estimate for a maximum density of individuals on the surface of a kelp forest (vulnerable to predation by kelp forest predators) during mass strandings, *Verella* represent an energy subsidy of 5.2 kJ/m² sea surface. While relatively little is known about the lipids and fatty acids of most hydrozoans, it has been shown that the dominant fatty acid in *Verella* is docosahexaenoic acid (DHA (22:6 ω 3) at ~28% of total fatty acids; Lopes et al. 2016). *Verella* also have relatively high proportion of eicosapentaenoic acid (EPA (20:5 ω 3) at ~8% of total FA; Lopes et al. 2016). DHA and EPA are considered to be key long-chain essential fatty acids in marine food webs because they are important for growth in many nearshore consumers, but most heterotrophs cannot synthesize these molecules de novo (Arts et al. 2001). The lipid contents of gelatinous zooplankton are generally known to vary greatly among taxa, on the order of ~4–12% of dry weight (e.g., Leone et al. 2015). Thus, large pulses of *Verella* biomass to coastal ecosystems could represent a significant input of essential fatty acids to these food webs.

Few data exist documenting the nearshore organisms that consume *Verella*. Hobson and Chess (1988) found *Verella* (among other pelagic hydrozoans) in the stomach contents of blue rockfish (*Sebastes mystinus*) during upwelling episodes, and it is likely that other species of kelp forest fishes consume *Verella* when high densities are available.

NEARSHORE ORGANISMS WITH A BIPARTITE LIFE HISTORY AS SUBSIDIES TO NEARSHORE ROCKY REEF HABITATS (MEROPLANKTONIC ORGANISMS)

Recruiting meroplanktonic organisms are the second category of cross-ecosystem trophic subsidy that must be considered as potentially influential for kelp forest food webs. Many organisms in nearshore Pacific Coast ecosystems live a bipartite life cycle that culminates in the kelp forest, spending a portion of their larval or juvenile life phase feeding and developing in the open ocean before recruiting to adult habitat (Figs. 2 and 3). Researchers have done extensive work

exploring population-level impacts of variation in recruitment of meroplankton, but few studies consider the impact of this variability on predator species that consume recruits, or the follow-on impacts to the general structure of nearshore food webs. Three examples of kelp forest species with bipartite life histories follow.

Juvenile rockfish (Sebastes spp.)

A prominent and visible annual subsidy to the kelp forest is that of juvenile rockfish recruits. More than 60 species of rockfish (*Sebastes* spp.) inhabit rocky reef and soft bottom marine habitats off the West coast of North America. The rockfishes are a major component of nearshore, shelf and slope fish assemblages and range from Alaska to the southern tip of Baja California, Mexico, on the West coast of North America (Love et al. 2002). Like many marine fishes, rockfish have a bipartite life cycle with pelagic larval and juvenile phases. Rockfish are live-bearers (viviparous), releasing 18,000–2,700,000 live larval fish per female that are immediately capable of feeding, though are able to survive for a short period of time on maternal-provided energy reserves (Love et al. 2002). The larvae eat and grow in the pelagic ocean, transitioning to juveniles before recruiting to their adult habitat. The pelagic larval phase lasts for 1–6 months as larvae grow from approximately 3–7 mm to approximately 15–90 mm at settlement (Love et al. 2002). Both stomach content analyses and stable isotope data support the hypothesis that juvenile rockfish facilitate substantial cross-shelf movement of carbon and other nutrients to the nearshore environment (Bosley et al. 2014).

The duration, magnitude, and frequency of the juvenile rockfish subsidy are well documented. On the West coast of North America, upwelling dynamics, advective transport, and internal waves lead to significant variability in the delivery of juvenile rockfish to the kelp forest (Carr 1991, Ainley 1993, Larson et al. 1994, Hobson et al. 2001, Caselle et al. 2010, Ralston et al. 2015). This impacts the annual availability of juvenile rockfish as a prey item and trophic subsidy to kelp forest predators. Particularly strong recruitment years (such as the mid to late 1980s, 2001 to 2003, and 2013) could represent a large pulse of nearshore productivity. Juvenile fish recruit to kelp forests in spring and summer

months and typically remain in the area for their adult life. Because this subsidy does not leave the kelp forest, the duration of availability of this subsidy for a given consumer can be described as the time between settlement and when a juvenile rockfish reaches a size that provides refuge from predation.

While we did not find explicit energy content estimates for post-settlement rockfish, juvenile rockfish in the pelagic environment represent an estimated 5.2–21.8 kcal/g dry mass (1.45–4.2 kcal/g wet mass) of energy (Vermeer and Cullen 1982, Perez 1994, van Pelt et al. 1997, Becker et al. 2007a, b, Glaser et al. 2015). Although highly variable in time and space, a heavy recruitment pulse can reach densities of 0.7 fish/m³ through the kelp forest water column, with densities in aggregations surrounding kelp plants and near the benthos much higher (Fig. 4; M. H. Carr, *unpublished data*). Using this estimate, pelagic energy delivered to the kelp forest in the form of juvenile rockfish could approach 23 kJ/m³. Because this is such a well-studied subsidy, juvenile rockfish allow us to take a landscape ecology approach to subsidies. The majority of ecological literature, including this review, considers a subsidy to be a unidirectional flow of energy. However, we can also look at a bidirectional flow (energy in vs. energy out) and calculate the net gain or loss of energy in a given system for a meroplanktonic subsidy. We have seen that the unidirectional flow of energy represented by recruiting rockfish to the kelp forest has the potential to be quite large, but what about the energy that left the kelp forest when larvae were advected to the open ocean? Do rockfish reproduction and the subsequent dispersal and recruitment back to kelp forest represent a net loss or net gain of energy to the system? A mature female rockfish produces 125,000–1.2 million (*S. melanops*)/16,000–640,000 (*S. caurinus*) larvae per reproductive event (Love et al. 2002). These larvae have a maternally provided yolk sac and an energy content of 0.345 calories (*S. melanops*)/0.688 cal (*S. caurinus*) at birth (Dygert and Gunderson 1991). Natural mortality rate in the pelagic ocean is estimated at 0.14/day, and the vast majority of larvae never return to the kelp forest after pelagic larval durations of 30–180 d (*S. melanops*)/30–60 d (*S. caurinus*; Tennera Environmental Services 2000, Carr and Syms

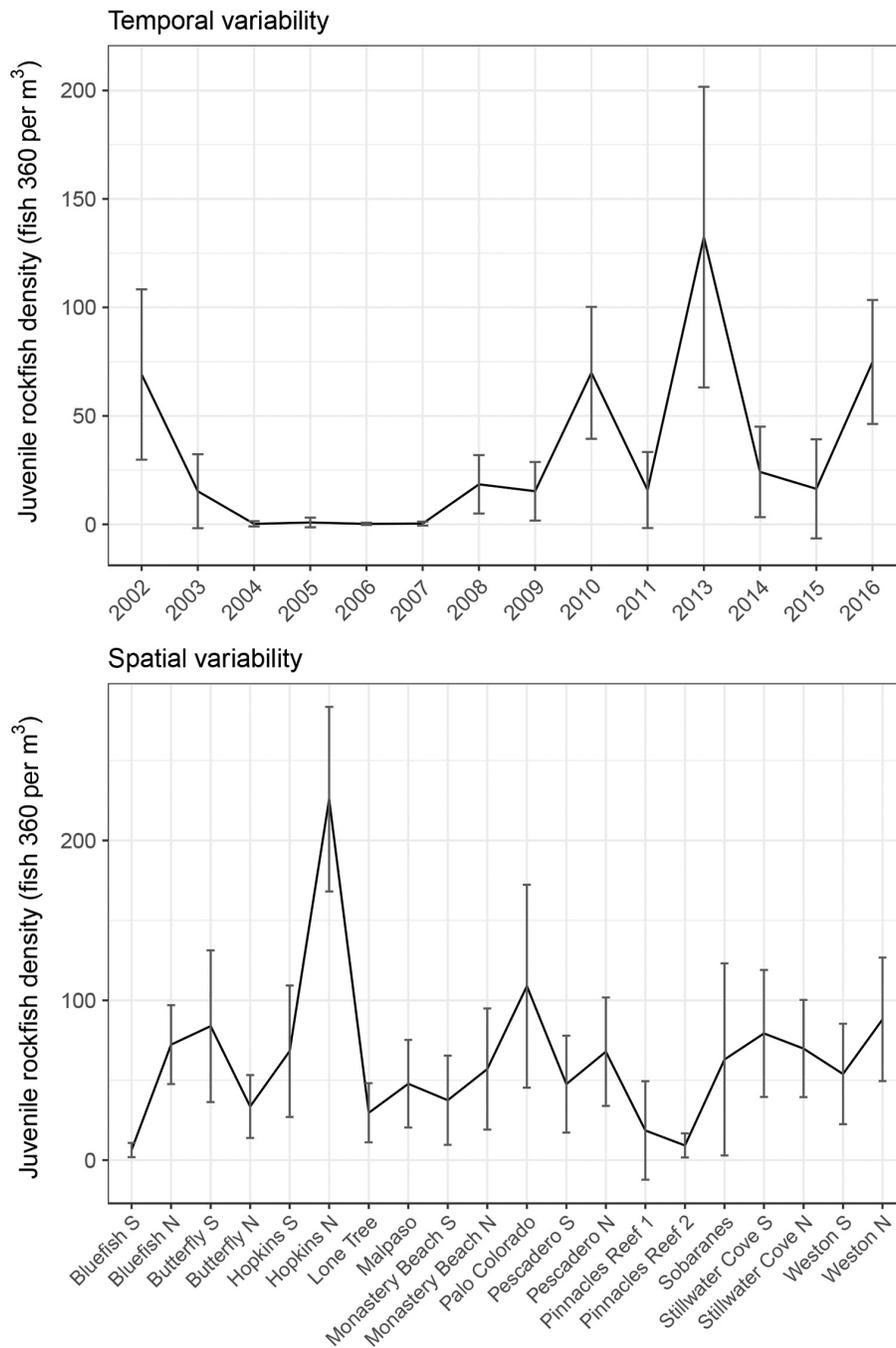


Fig. 4. Spatial and temporal variability in the density of juvenile rockfish in the kelp forest water column. Error bars represent one standard deviation. (Top) Temporal variability is demonstrated with the time series of rockfish recruitment data from Stillwater Cove, Carmel Bay, California. (Bottom) Spatial variability is demonstrated with rockfish recruitment data from sites in and around Carmel Bay in 2010. For locations of sites, visit www.piscesweb.org.

2006, Ralston et al. 2013). Using mean fecundity and pelagic larval duration values for calculations, and with an energy content of 4.2 kcal/g for recruiting juvenile fish, we estimate that rockfish reproduction represents a net gain (in the case of *S. caurinus*) and a net loss (in the case of *S. melanops*) of energy to the kelp forest (Fig. 5). Due to species differences and the wide range of annual larval production and of potential pelagic larval durations, it is reasonable to consider that this reciprocal subsidy represents no net change in total annual energy for kelp forest ecosystems, though the offset timing of subsidy exit to the open ocean and arrival to the kelp forest is undoubtedly important (Takimoto et al. 2002, Sato et al. 2016).

In their pelagic environment, larval and juvenile rockfish are a major food source for seabirds and other predators (Mills et al. 2007). Becker et al. (2007a, b) explored impacts of variation in juvenile rockfish availability for marbled murrelet (*Brachyramphus marmoratus*) reproduction, finding that murrelet productivity was positively

correlated with juvenile rockfish (and krill) abundance. Post-recruitment juvenile rockfish are also an important and high-quality food source for a wide range of kelp-associated species, particularly adult rockfish and other predatory fish (e.g., lingcod, *Ophiodon elongatus*) (Hallacher and Roberts 1985, Hobson et al. 2001, Johnson 2006, Beaudreau and Essington 2007, Tinus 2012). The group of rockfish species that inhabit nearshore rocky reefs as adults recruit to several microhabitats within kelp forest systems, expanding the accessibility of juvenile rockfish prey to a large group of predators (Carr 1991, Love et al. 1991).

Juvenile Dungeness crabs (*Metacarcinus magister*)

The vast majority of shallow subtidal and intertidal West coast marine invertebrates have a pelagic larval phase before they recruit back to nearshore habitats. Among these is the ecologically and economically important Dungeness crab, *Metacarcinus magister*, a crustacean that uses broadcast spawning to release meroplanktonic

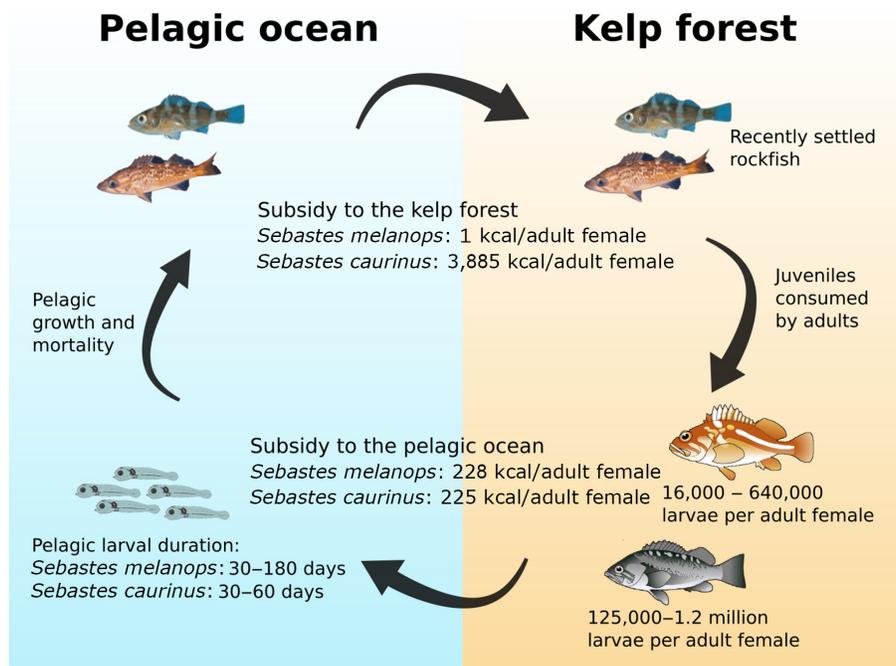


Fig. 5. The net energy flow away from and back to the kelp forest ecosystem resulting from rockfish reproduction and the subsequent recruitment of larvae varies by species (see *Juvenile rockfish (Sebastes spp.)* section for specifics regarding calculations). It is important to note that juvenile rockfish disperse widely and are not likely to return to the same kelp forest where they were born.

larvae with initially limited swimming ability. In the Pacific Northwest, juveniles complete a pelagic life phase in the plankton and settle to near-shore and estuarine habitats from March to November, with peak recruitment typically occurring from May to June (Roegner et al. 2003, 2007). Settlement of this species occurs in distinct pulses at approximately two-week intervals that last for several days (McConnaughey et al. 1992, Roegner et al. 2007, Shanks et al. 2010).

Not only is this a pulsed subsidy, the magnitude of annual recruitment is also extremely variable. Trawl surveys off the Washington coast showed that settlement to the nearshore environment varied nearly 40-fold from year to year (1983–1988), while surveys in Oregon showed that recruitment varies by a factor of more than 1000 (McConnaughey et al. 1992, Shanks 2013). This extreme variation in year-class abundance is a result of interannual variation in coastal circulation, timing of the spring transition, and upwelling strength and undoubtedly influences the nearshore food webs to which they settle (McConnaughey et al. 1992, Shanks 2013). A 12-yr data set of daily abundance of Dungeness crab megalopae in Coos Bay, Oregon, USA, showed a clear effect of the Pacific Decadal Oscillation phase on crab abundance with higher abundances during years of negative PDO (Shanks 2013). In addition, researchers found a negative correlation between megalopae abundance and timing of spring transition in the California Current, the shift from winter downwelling to spring upwelling (an early spring transition leads to a higher return of Dungeness megalopae), and a positive correlation between abundance and upwelling during settlement season (Shanks 2013). Likely representative of the complex oceanographic dynamics driving variability in the delivery of larvae of many nearshore species, recent work has concluded that while upwelling plays a major role in transporting the larval crabs from the open ocean to the continental shelf, internal tides and other coast-associated mechanisms transport the megalopae to their settlement habitat (Shanks 2013). Density of post-recruitment juvenile crabs also varies by habitat, substrate type, and depth. Crab densities tend to decrease as depth and distance from shore increase, and as substrate coarseness increases (McConnaughey et al. 1992). Despite an

expected preference for silty or sandy habitats relative to gravel (and presumably rocky) substrates, post-larval crabs seem to use a wide diversity of habitats in years with large recruitment events (Eggleston and Armstrong 1995, Galloway et al. 2017). One such very large recruitment event occurred off the coast of Oregon in April 2016, with densities of new recruits exceeding 20,000 individuals/m² in one layer of crabs in an area where crabs were stacked up to three layers deep (Galloway et al. 2017). This observation, collected using SCUBA, was corroborated by other anecdotal observations (ROV videos, reports from fishers, intertidal observations) collected at other locations on the Oregon coast in the spring of 2016 and in lesser numbers in the summer of 2008 (Fig. 3b; Galloway et al. 2017).

Crustaceans are considered to be high-value prey items, and Dungeness crabs are no exception. Since we found no published energy content information for a Dungeness crab juvenile, we use an estimate of 2.37 (± 0.14) J/individual, measured for spider crab (*Hyas araneus*) megalopae (Anger and Dawirs 1982). With the extraordinarily high densities of recruits observed in nearshore subtidal habitats (estimates of 20,000–65,000 crabs/m²), a single recruitment pulse could contribute 47 kJ/m² of energy to the nearshore system, based on the lower end of this observed range of densities described in Galloway et al. (2017) and the energy density estimate above (kJ). The total lipid content for Dungeness crab megalopae is very high (~15% of total dry weight) but quickly declines (e.g., to ~4–5%) within a few weeks of settlement (A. W. E. Galloway, unpublished data). Similar to the pelagic red crab, Dungeness crab have relatively high essential ω -3 fatty acid content, and total lipid content of adult crabs at ~1% of total dry weight (King et al. 1990).

Though the majority of evidence for the trophic importance of Dungeness crab juveniles comes from estuarine and pelagic habitats, these observations give us insight into possible kelp forest predators. Research supports predation, including cannibalism, as the major driver of rapid declines in abundance of newly settled Dungeness crabs in the months following settlement (Armstrong et al. 1995). Of seventy demersal and pelagic fishes sampled in central

California, 21 had Dungeness crab megalopae, young-of-the-year post-settlement instar, or older age class stomach contents (Reilly 1983). Many kelp forest fishes are generalist predators, limited primarily by their gape and the size of potential prey. Based on this evidence, we predict that kelp forest fishes (e.g., rockfishes in the genus *Sebastes*, surfperches of the family Embiotocidae) consume juvenile Dungeness crabs, especially during large recruitment events. In support of this hypothesis, Galloway et al. (2017) sampled black rockfish (*Sebastes melanops*) during the previously described 2016 large Dungeness crab recruitment to the nearshore and observed that a large proportion of fish captured had eaten so many juvenile crabs that they regurgitated the megalopae at the surface. Moreover, divers observed events of cannibalism in situ, on the rocky reef where the initial settlement occurred; several adult Dungeness crabs were found on the rocky ledges, eating the settlers (Galloway et al. 2017; *personal observations*). A study in northern California shows Dungeness crab megalopae and post-larval instars to also be important prey for copper rockfish (*Sebastes caurinus*; Prince and Gotshall 1972). In the estuarine environment, ample evidence supports the widespread predation on newly settled Dungeness crabs by the staghorn sculpin (*Leptocottus armatus*), a species similar to the many species of the family Cottidae in the kelp forest ecosystem (Armstrong et al. 1995). Several other fish species, wading birds, and larger crabs join the staghorn sculpin as important predators benefitting from the delivery of larval crabs to nearshore habitats (Stevens et al. 1982, Fernandez et al. 1993).

Herring (*Clupea pallasii*) eggs

While adult Pacific herring returning to nearshore spawning habitats are a trophic subsidy themselves, herring eggs provide a distinct and extraordinarily rich subsidy to seagrass beds and kelp forests from California to Alaska (Fox et al. 2018). Like many pelagic fishes, herring females deposit tens of thousands of small, adhesive eggs onto subtidal vegetation, rocks, shells, and man-made structures (Watters et al. 2004). Spawning takes place in the spring months (though as early as December in California, and as late as June in Alaska) and typically happens over 3 to 6 weeks and in several pulses at a given

location (Willson and Womble 2006). Prince William Sound spawning was highly variable during the period of 1973–1999 but seemed to have a 4-yr cycle (Norcross and Brown 2001). Eggs hatch quickly in 1.5–3 weeks, giving predators only a short time to consume available eggs (Willson and Womble 2006).

Due to the economic and cultural importance of herring runs throughout their range, and the tight coupling between spawn and the current spawning stock biomass, the herring egg subsidy has been very well quantified by research and monitoring spanning almost a century, including the diver and aerial surveys done today (Schweigert 1993, Hay et al. 2009). Using this information, Paul et al. (1996) conducted an investigation into how the Exxon Valdez oil spill impacted the herring egg subsidy to nearshore environments in Prince William Sound. By counting eggs in adult females directly before spawning, they estimated that the approximate energy delivered to nearshore habitats (including both kelp forest and seagrass habitats) in the form of eggs (with an estimated energy content of 8.1 J energy/egg [± 0.9 standard deviation]) prior to the oil spill was 68×10^9 kJ (Paul et al. 1996, Paul and Paul 1998). Along with this vast influx of energy, elevated levels of DHA and EPA in consumers suggest fatty acid contributions from pelagic influx and spawning of herring which are known for their high levels of these fatty acids (Fox et al. 2014, Moss 2016).

Predation on herring spawn, particularly predation by birds, has been a focus of research for nearly 100 yr (Munro and Clemens 1931, Schweigert and Haegerle 2001). On the Pacific coast of North America, predation is a major source of herring egg loss with seabirds and ducks consuming a substantial proportion of annual herring spawn, including herring spawn from kelp forests. Using a fecal analysis and a bioenergetics model, Bishop and Green (2001) estimate that the five most abundant seabird species in Prince William Sound consumed approximately 31% of all eggs deposited in 1994. Not surprisingly, bird predation on herring eggs provides an example of population-level impacts of a cross-ecosystem subsidy. Several studies have shown depth to be an important predictor of egg mortality, providing another indication that avian predation may play an especially critical role in egg survival,

and that birds are likely major benefactors of this subsidy (Norcross and Brown 2001, Schweigert and Haegele 2001). In addition to avian predation, generalist fish and invertebrate predators are common in both intertidal and shallow subtidal zones where herring eggs occur. Herring off the Norwegian coast exhibit a similar spawning pattern to fish in British Columbia, depositing eggs that are then prey for benthic fish predators such as haddock (*Melanogrammus aeglefinus*), and benthic crustaceans (Varpe et al. 2005). Using a stomach content analysis of potential fish predators, hexagrammid fishes were estimated to consume 2–9% of herring eggs in Prince William Sound (Rooper 1996). Haegele (1993) estimated that epibenthic invertebrates spanning many taxa (though the predominant predators were crabs) consumed 3.7% of total herring eggs at several sites in British Columbia. An interesting comparison can be made between the herring egg subsidy, and the energy-rich eggs of cisco (*Coregonus artedii*) that bring energy from pelagic waters to nearshore benthic communities in Lake Superior (Stockwell et al. 2014). The cisco egg subsidy was shown to represent 79% of the energy consumed by whitefish (*Coregonus clupeaformis*; a nearshore benthic fish) in the winter months and led to an observed increase in lipid stocks during the winter, rather than the predicted decrease (Stockwell et al. 2014).

POPULATION- AND COMMUNITY-LEVEL CONSEQUENCES

Today we see calls to advance our quantitative understanding of the effects of cross-ecosystem subsidies (Richardson and Wipfli 2016). There is wide recognition that subsidies result in ecological consequences at varying levels of organization, and in general, observational and experimental approaches have shown positive consumer responses to trophic subsidies (Polis et al. 1997, Marczak et al. 2007). However, characteristics of both trophic subsidies and organisms that consume these subsidies impact the response that consumers and populations will have (Yang et al. 2008; Table 3). The duration of a subsidy pulse and the size of the subsidy organism relative to the size of potential consumers in the recipient ecosystem are important when predicting the influence of that subsidy.

Similarly, attributes of a consumer, such as feeding mode, will determine whether it is able to exploit a certain subsidy and how that subsidy might impact individual consumers and/or the consumer population. Finally, attributes of the recipient system, for instance, what nutrients are limiting, will play a role in the consequences that result from the delivery of trophic subsidies. Importantly, spatial resource subsidies are donor-controlled, meaning that the recipient can often consume all or most of the subsidy and cannot affect the magnitude of future subsidy inputs. In other words, subsidy source populations are decoupled from consumer dynamics in the recipient system.

Attributes of resource inputs affect ecosystem response

As the rate of delivery, timing, frequency, form (e.g., eggs vs. larvae), dispersion (i.e., patchiness), and magnitude of subsidy inputs change, the response of consumers may shift. The ways that these individual attributes of resource inputs might influence kelp forest responses can be explored based on research findings in other ecosystems. Studying the sockeye salmon egg subsidy in aquatic systems, researchers showed that temperature and subsidy presence interact to influence predator (juvenile coho salmon) size and fatty acid composition (Smits et al. 2016). Moreover, consumer and aquatic ecosystem responses to subsidies depend on the timing of subsidy deliveries in relation to autochthonous prey production (Sato et al. 2016). Changes in the timing of subsidy resources in relation to the life history of a consumer can lead to variation in ecosystem responses as well. For example, riparian spiders that receive subsidy resources early in development are at a disadvantage relative to those that receive subsidies closer to reproduction (Marczak and Richardson 2008). Though there have been fewer empirical studies looking at the effect of variable magnitude and frequency of subsidies, it is likely that these attributes also play a role in determining ecosystem response.

Consumer attributes influence individual- and population-level effects of subsidy resources

The impact that a pulsed resource has on a consumer species will be highly dependent on

Table 3. Characteristics of (a) the recipient ecosystem, (b–c) the resource inputs, and (d) specific consumers influence the relative importance and consequences of a cross-ecosystem trophic subsidy.

Attributes	Related Considerations	Examples
(a) Recipient ecosystem		
Trophic complexity	Subsidy causing indirect impacts up or down the food chain	Bustamente et al. (1995); Polis and Hurd (1996); Maron et al. (2006)
Limiting nutrients in the recipient system	Variability of nutrient limitation; whether the subsidy provides a limiting nutrient	Anderson and Polis (1999); Adame et al. (2015)
In situ productivity, baseline nutrient levels	In situ energy production relative to energy delivered with the subsidy	Anderson and Polis (1998); Marczak et al. (2007)
Perimeter-to-area ratio and other landscape features	Connectivity with other ecosystems; exposure to physical forces	Polis and Hurd (1996)
Physical environment	The impact of temperature, geomorphology, hydrodynamics, and other physical attributes	Orr et al. (2005); Smits et al. (2016); Morgan et al. (2018); Armstrong et al. (2010)
(b) Subsidy delivery		
Duration	Duration of subsidy (how long it remains in the recipient system) relative to the response rate of potential consumers	
Timing	Timing relative to the timing of other prey items (i.e., when other prey is abundant or scarce) and demand by consumers in the recipient system (e.g., during periods of growth or reproduction)	Takimoto et al. (2002); McCormick (2003); Wright et al. (2013); Sato et al. (2016)
Frequency	The greater the frequency, the more likely subsidies will coincide with timing of need by consumers, who will adapt foraging responses	Anderson et al. (2008); Trebilco et al. (2016)
Predictability	Consumer species may have evolved to use a predictable subsidy	Armstrong and Bond (2013)
Magnitude	Energy content relative to in situ energy production; whether the subsidy is delivered in pulses	Janetski et al. (2009); Spiller et al. (2010); Marcarelli et al. (2011)
Density		Moore et al. (2008)
Spatial extent and evenness/patchiness	Patchiness and the spatial match or mismatch with consumers	Meyer and Schultz (1985)
(c) Subsidy organisms		
Quality	Nitrogen, Carbon, lipid and energy content, content of specific fatty acids and other nutrients, bioavailability of the subsidy	Anderson and Polis (1999); Marcarelli et al. (2011); van Deurs et al. (2016)
Palatability, digestibility		Rodil et al. (2015); Dethier et al. (2014)
Size relative to consumer size	Whether a consumer can consume the subsidy	Marczak et al. (2008)
Ability to evade predators	Whether the consumer is able to capture and handle the subsidy organism	
Position in the water column	Physical location in the water column (especially relative to consumer foraging location)	Orr et al. (2005)
Trophic level		Leroux and Loreau (2008)
(d) Subsidy consumers		
Limiting nutrients	Whether the subsidy delivers a limiting nutrient that might increase growth or impact reproduction of the consumer	van Deurs et al. (2016)
Generation time	Generation time of the consumer relative to subsidy pulse frequency and duration	Yang et al. (2008); Holt (2008)
Mobility	Ability of a consumer to access a remote subsidy	Paetzold et al. (2008); Mellbrand et al. (2011)
Size	Gape width and prey size selectivity	van Deurs et al. (2016)
Conversion rate/assimilation efficiency		Small et al. (2013); Richardson and Wipfli (2016)
Functional response to subsidy resources		Richardson and Wipfli (2016)

(Table 3. Continued.)

Attributes	Related Considerations	Examples
Trophic level		Leroux and Loreau (2008)
Trophic ecology (i.e., generalist or specialist)	Whether the consumer is specialized on subsidy prey or a given subsidy species	
Feeding mode		Netto and Meneghel (2014); Von Biela et al. (2016)
Habitat utilization		Beaudreau and Essington (2011)
Anatomy and physiology		Armstrong and Bond (2013)
Life history characteristics (e.g., growth rate)		Nowlin et al. (2008)
Prey preference		Leroux and Loreau (2008)

the particular life history of that consumer. Long-lived predators such as kelp forest rockfishes (genus: *Sebastes*) will be less likely to respond to a pulsed subsidy with short-term increases in abundance, but may exhibit increases in growth or reproduction, depending on the timing of subsidy availability. Larson (1991) describes a remarkable trophic subsidy of pelagic red crabs to nearshore California environments. During this period, fat and liver weights of *Sebastes* spp. increased, and the researchers posit that the subsidy-related change in food availability positively affected reproduction. In contrast, short-lived and fast-reproducing species, such as many kelp forest invertebrates, might be expected to respond to abundant subsidy resources with a more rapid numerical response. For both long- and short-lived species, the generality of these responses should be tested.

The expected consumer response to a subsidy will also depend on that consumer's trophic level, foraging habits, behavior, and size and age class (Anderson and Polis 2004, Marczak et al. 2007, Richardson and Wipfli 2016). Because subsidies are not always present in recipient ecosystems, few consumers specialize on individual subsidy sources of prey (Ostfeld and Keesing 2000). As a result, trophic benefits of subsidies likely accrue first to generalist consumers with the ability to switch prey types when abundant and high-quality subsidy resources are available (Yang et al. 2008). Coutré et al. (2015) explored the use of seasonally pulsed, high-energy trophic subsidies by juvenile sablefish (*Anoplopoma fimbria*), concluding that the fish consume high-energy subsidies when they are available, but are

not entirely reliant on this food source. However, this is not always the case. The Dolly Varden (*Salvelinus malma*) fish exhibits unique physiological adaptations that allow it to specialize on the highly predictable subsidy of riverine salmon eggs, making them very reliant on this allochthonous food source (Armstrong and Bond 2013). Mobility will also play a major role in the functional and aggregative response of a consumer to a subsidy resource. The consumer must be able to encounter and exploit the subsidy resource on the temporal and spatial scales that the resource is retained in the kelp forest and available.

Ecosystem-level effects of subsidy resources

Using a meta-analysis of 115 data sets from 32 studies of consumer responses to ecosystem subsidies, Marczak et al. (2007) make several important conclusions about consumer–subsidy interactions. First, consumer response is significantly related to the ratio of subsidy resources to comparable resources in the recipient system, but the strength of consumer response cannot be predicted by the productivity of the recipient ecosystem. This observation underscores the importance of quantifying subsidy inputs for kelp forest food web modeling. Second, subsidies will likely be more impactful in recipient ecosystems with high perimeter-to-area ratios (or surface area-to-volume ratios in three-dimensional marine environments), though duration of retention of the subsidy in the recipient system is also influential. Patchy distribution of kelp forests interspersed with other habitats often leads to a high surface area-to-volume ratio, with much of the forest directly exposed to outside influences.

This indicates that subsidy resources may play an especially important role in kelp forest trophic ecology. Broad generalizations such as the relationship between the surface area-to-volume ratio and subsidy importance are beginning to emerge, providing a platform for future experimental and observational studies that address subsidy impacts.

Many studies support the expectation that trophic coupling of adjacent (or otherwise spatially coupled) marine ecosystems impacts everything from predator–prey dynamics to community composition in recipient ecosystems (e.g., Bustamente et al. 1995, Sabo and Power 2002, Takimoto et al. 2002). Evidence now suggests that subsidies can impact the distribution, relative abundance, and density of recipient species, with some subsidized marine consumers maintaining higher population densities than would exist without subsidy resources. Abyssal sharks, fishes, and other organisms benefit from the infrequent but energy-rich influx from whale falls and wood falls, maintaining densities that would not be possible with only the sparse resources available in the deep sea (Bennett et al. 1994, Koslow et al. 2000, McClain et al. 2018). Pulses of gelatinous zooplankton increase the abundance (with a two-year lag) of two deep-water benthic detritivores (Atlantic hagfish and grenadier; Smith et al. 2016). And in the kelp forest, foraging movements and distribution patterns of a planktivorous damselfish (*Chromis punctipinnis*) depend on the direction of current flow that delivers plankton subsidies into the forest (Bray 1981, Kingsford and MacDiarmid 1988).

The most apparent impact that subsidies have on recipient ecosystems is their influence on trophic interactions. Subsidies can completely or partially decouple consumers from in situ prey population dynamics, and researchers have suggested that the intensity of species interactions is influenced by subsidy delivery rates (Menge et al. 2003). However, many food web studies and models remain limited to a single ecosystem, ignoring the impact of subsidy resources. Focusing on consequences of cross-ecosystem resource subsidies in aquatic systems, Richardson and Wipfli (2016) describe four potential functional responses of the direct consumers of trophic subsidies. These include response shapes that model prey switching, prey-swamping and/or

saturation, and the simple linear increase in consumer response as subsidy availability increases (Holling 1959). For example, predators subsidized by outside energy sources might consume fewer kelp forest prey items, thereby releasing those organisms from predation. Sea otters (*Enhydra lutris*) at Amchitka Island, Alaska, undergo a drastic dietary switch from kelp forest fishes to the episodically abundant Pacific smooth lump sucker (*Aptocyclus ventricosus*) and benthic invertebrates, with the subsidy resource leading to an increased foraging profitability for the otters (Watt et al. 2000). Alternately, any increase in predator abundance in response to subsidy resources could lead to increased predation on kelp forest organisms via apparent competition (Holt 1977, Schmitt 1987). In addition to this diversity of responses that might be expected from direct consumers, impacts will propagate throughout the food chain via top-down and bottom-up forces. When consumers exhibit numerical responses to pulses of subsidy resources, these population changes are likely to have follow-on effects on other prey sources, competitors, their predators, and even parasites and pathogens in the system (Ostfeld and Keesing 2000). In their review on the ecosystem-level impacts of migratory animals (a temporally predictable subsidy), Bauer and Hoye (2014) identify instances where the timing of consumer reproduction and predator–prey interactions of non-subsidy species are structured by the presence of migrants (a trophic subsidy in this case).

For further insight into the effects of pelagic subsidies on kelp forest ecosystems, we can look to several decades of work in the rocky intertidal ecosystem (Bustamente et al. 1995, Menge et al. 1997, 2003, Krenz et al. 2011). Trophic connectivity between the pelagic ocean and the intertidal zone (often termed benthic–pelagic coupling) is mediated by oceanographic currents and other physical dynamics and can provide insights into expected pelagic–kelp forest subsidy responses. Krenz et al. (2011) measured both larval settlement and delivery of particulates to intertidal environments on the West coast of North America, determining that subsidy dynamics are highly spatially variable, and suggesting that this plays a role in driving the observed latitudinal gradients in community structure. These breaks along the coast in terms of the importance of

subsidies to marine ecosystems might apply to kelp forests as well. In South Africa, subtidal kelps subsidize intertidal limpet populations, allowing them to reach much higher densities than they otherwise would. Because limpets are primary space holders, increases in their density lead to follow-on impacts to community structure (i.e., subsidized limpets are able to keep the intertidal clear of understory algae) and function of the entire intertidal community (Bustamente et al. 1995). Describing subtidal–intertidal coupling, Gaines and Roughgarden (1985, 1987) showed that predation on recruiting barnacle nauplii by juvenile rockfish in the kelp forest leads to a decrease in intertidal barnacle recruitment. This decline in recruitment certainly impacts other intertidal species, and similar processes likely exist for organisms recruiting to kelp forest habitats.

Studies of consumer and ecosystem responses to subsidies in the kelp forest are rare but increasing. In an explicit look at the role that pelagic–benthic coupling plays on the nearshore, rocky reef habitats of Chile, Docmac et al. (2017) use carbon stable isotopes to conclude that the dominant trophic pathway for kelp forest fishes is based on pelagic energy. Though further work is necessary to determine the mechanisms for the delivery of this pelagic-based energy, the results imply that subsidies are quite important. Beaudreau and Essington (2007) quantify the diet of lingcod (*Ophiodon elongatus*), an important kelp forest predator, finding that pelagic fish in the family Clupeidae (such as Pacific herring) were the second most numerically abundant prey family. In a follow-up paper, they use movement data to show that this transfer of energy from the pelagic ocean to the nearshore is prey-mediated rather than a result of lingcod foraging runs to offshore habitats (Beaudreau and Essington 2011). Hobson and Chess (1988) linked periods of summer downwelling in northern California and the influx of gelatinous zooplankters to instances of full stomachs in blue rockfish (*Sebastes mystinus*), highlighting the importance of these pulses. A recent hypothesis put forward by Trebilco et al. (2016) suggests that cross-ecosystem trophic subsidies may enable the inverted biomass pyramid structure seen in relatively pristine coral reef and kelp forest ecosystems.

HOW DO WE MEASURE THESE SUBSIDIES AND THEIR EFFECTS ON NEARSHORE SYSTEMS?

At the most basic level, we need metrics of the timing, duration, magnitude, and frequency of pelagic ocean subsidies to nearshore systems, characteristics that can directly influence impacts to individuals and populations. Consumers might evolve to use subsidy resources, particularly those that are predictable, but there are many components of uncertainty for those subsidies that come infrequently as unpredictable pulses. The timing of a subsidy might coincide with increased energy requirements for a consumer during a reproductive season or might be less important because of a timing mismatch between the subsidy and consumer needs. A subsidy of very large magnitude over several weeks might induce a shift in foraging habitat for mobile predators, while the impacts of a shorter-term influx of smaller magnitude might remain more localized. Once a general understanding of subsidy dynamics is established, additional information is necessary to predict subsidy impacts. Data on the nutritional quality and palatability of subsidy resources for consumers, and an understanding of the likelihood that subsidy resources will be consumed, is a next step. Subsequent studies can then address numerous other system attributes and factors that will influence potential ecological impacts of a subsidy resource (Table 3).

One of the inherent challenges to quantifying cross-ecosystem subsidies, especially those that move from the pelagic ocean to the nearshore kelp forest, is the interdisciplinary data collection involved. There is currently a mismatch between the scale at which oceanographic data relevant to kelp forests are collected (data important to understand subsidy dynamics) and the scale at which ecological data in nearshore environments are collected (data essential for understanding community and population impacts of these subsidies). Oceanographers often focus on ocean basin, large-scale processes at scales too large for observation of the movement of subsidy organisms on a weekly or monthly time frame. Kelp forest ecologists often conduct short-term experimental and observational studies at the level of the individual forest, using SCUBA transects to quantify ecosystem changes. These methods are

not always suitable for observing episodic influences or quantifying rates of delivery of subsidy organisms (especially those not easily observed) and are not always representative samples of the broader geographic significance. In addition, studies over a few years may not be long enough to capture variation in subsidies and resulting impacts to trophic dynamics. This suggests that the development of sampling methods and designs that integrate over time, such as time-lapse video equipment that can sample frequently over long periods, will be beneficial. Finally, while separating and simplifying ecosystems is extremely useful for many studies, engaging experts across traditionally drawn ecosystem boundaries and disciplines is necessary to truly understand connectivity and the functioning of ecosystems (Saunders et al. 2015).

With many organisms that are commonly important as coastal resource subsidies to other consumers, we tend to quantify impacts in only the most visible or accessible habitats. For example, Dungeness crab recruits have been counted in many estuarine zones, but largely ignored in nearshore subtidal areas (Armstrong et al. 2003, Galloway et al. 2017). Similarly, we have a wealth of data on the dynamics of barnacle recruitment to the rocky intertidal, but no analog exists for barnacle recruitment to subtidal reefs, despite evidence for pulses of barnacle recruits large enough to impact kelp forest food webs. Understanding the diversity of settlement habitats for nearshore organisms will not only benefit our understanding of those populations, but also give insight into the spatial scale and timing at which the subsidy might be important.

As demonstrated in the six examples above, the dynamics of cross-ecosystem subsidies vary dramatically from one organism and location to another. Some organisms recruit from the open ocean to the kelp forest during downwelling conditions, while upwelling conditions bring others to the nearshore environment (Mace and Morgan 2006, Caselle et al. 2010). Certain subsidy organisms (e.g., pelagic red crabs in Monterey Bay) are found in kelp forest systems only during El Niño years when other food sources for kelp forest predators are less abundant (McClatchie et al. 2016). More work is needed to understand how the subsidies interact with each other and with other kelp forest energy sources (Anderson et al.

2008). Does a subsidy asynchronous with intrinsic resource production stabilize consumer–resource interactions by ensuring more consistent food resources for kelp forest predators in a variable ocean environment? Or do subsidies synchronous with intrinsic production represent extra energy when the subsidy pulses arrive (i.e., do subsidies that coincide with high periods of intrinsic productivity amount to wasted energy)? Do subsidies always represent additional prey resources or do they sometimes simply decrease the time and energy (foraging costs) it takes for a consumer to find prey?

It is clear that our understanding of food webs could benefit from increased understanding of subsidy organisms; however, the most efficient and useful time, place, and method to make measurements are not always obvious. Ongoing efforts, such as monitoring done by the National Marine Fisheries Service and California Cooperative Oceanic Fisheries Investigations (CalCOFI), in the California Current ecosystem measure densities and relative abundance of potential kelp forest subsidy organisms while in their pelagic habitats. This is useful, but several issues arise when using these measurements to infer the realized magnitude of a subsidy. The vast majority of meroplanktonic organisms will be consumed or otherwise die before settling to nearshore habitats. In addition, complex movement of organisms in the pelagic phase of a bipartite life cycle means that a subsidy may not be expected in nearshore environments directly adjacent to their offshore presence. To translate pelagic density measurements to nearshore densities at useful temporal scales, we need both reasonable estimates of pelagic mortality and an understanding of pelagic movement and settlement dynamics. Holoplanktonic organisms may live their entire life cycle in pelagic environments or might be swept to nearshore habitats and represent subsidy resources, but we often lack an understanding of the oceanographic forces that determine when advection to nearshore environments will occur (but see Roegner et al. 2003). When paired with local-scale measurements of ocean conditions, and an improved understanding of the oceanographic forces that move pelagic organisms to the nearshore environment, these measurements of offshore densities (or simply presence and absence data) can prove useful

for determining subsidy timing and location. As demonstrated by Morgan et al. (2018) in the surf zone and intertidal environments, measurements of abiotic forces (e.g., currents, internal waves) can alert ecologists to locations, seasons, and years where subsidies might be especially influential. Understanding the patterns of heterogeneity inherent in the oceanographic conditions in kelp forest ecosystems (e.g., variation in upwelling strength, which plays a major role in determining delivery of pelagic materials) is a great starting point for predicting what reefs might be especially reliant on trophic subsidies (Pérez-Matus et al. 2017). However, the most reliable way to measure pelagic subsidies remains obtaining estimates of the abundance and timing of these organisms in kelp forest ecosystems.

There are several widespread ways that researchers are currently quantifying organisms that represent cross-ecosystem subsidies. Ecologists along the West coast of North America routinely deploy standardized units for the recruitment of fishes or SMURFs to measure delivery of juvenile rockfish to kelp forest habitats (Ammann 2004). The Partnership for the Interdisciplinary Study of Coastal Oceans (PISCO) and Reef Check California conduct annual diver surveys in kelp forests where juvenile rockfish are counted and measured. Shanks and others commonly deploy light traps to collect invertebrate larvae (e.g., Dungeness crab larvae) as they recruit to nearshore systems, and many groups use recruitment tiles for the ongoing monitoring of invertebrate larval delivery to nearshore marine habitats (Shanks 2009, Shanks et al. 2010). However, the behaviors and physical forms of certain organisms (especially gelatinous organisms) do not lend themselves to detection by these traditional methods of recruitment monitoring. For these organisms and for more easily observed subsidies, researchers often rely on indirect measurements such as analysis of stomach contents of predators (Coutré et al. 2015, Smith et al. 2016, Eriksen et al. 2018). We can further use stomach content information to better understand the role of prey switching in consumer organisms, how a switch might correspond to the timing of a subsidy or availability of resident prey, and whether prey switching is dependent on age or size of the consumer

(Hobson and Chess 1988, Watt et al. 2000). Other creative methods have been used to infer the delivery, frequency, and magnitude of subsidies. Monitoring of oceanographic conditions and water chemistry measurements can illuminate likely locations and timing of the delivery of subsidies (Shanks et al. 2000, Sponaugle et al. 2002). Additional monitoring of predator diets through the use of stable isotope and fatty acid analysis allows researchers to infer use of subsidies and potential food web and community-level impacts (Stapp and Polis 2003, McMahon et al. 2016). For example, using both C and N isotopic values for two kelp forest fishes, Von Biela et al. (2016) estimate kelp-derived carbon to make up 36–89% of the diet of the benthic feeding kelp greenling (*Hexagrammos decagrammus*) and 32–65% of the more pelagic-dwelling black rockfish. Others have used stable isotopes and food web models to examine the relative importance of pelagic- vs. macroalgae-derived carbon to secondary production in kelp forests (Duggins et al. 1989, Koenigs et al. 2015, Docmac et al. 2017, Truong et al. 2017).

To make basic information about subsidy dynamics relevant to our understanding of the trophic ecology of recipient ecosystems, information about the energy content, proximate composition, and presence of any nutrients or molecules (e.g., certain fatty acids) that are rare or limiting in recipient systems is useful. As demonstrated with the calculations above, data to examine the energetic contributions made by subsidies and the quality of these inputs to recipient kelp forest ecosystems are not always readily available. Publication of energy content estimates from calorimetry measurements or proximate composition analysis is essential to continued work on the ecology of kelp forest subsidies, and we should renew efforts to develop these basic estimates for poorly studied organisms (such as gelatinous zooplankton). Researchers should also consider the role of dietary lipids and particular fatty acids delivered with a subsidy. For example, resources that are rich in long-chain, ω -3 fatty acids are often extremely valuable prey for consumers (Winder et al. 2017), which cannot otherwise synthesize these “essential” molecules *de novo* (see Arts et al. 2001, Dalsgaard et al. 2003). These nutritionally valuable resources may only be delivered to consumers in discrete intervals at

certain times of the year, such as salmon returning to spawn in natal streams, delivering essential fatty acids to terrestrial river and forest food webs (Heintz et al. 2004). van Deurs et al. (2016) traced important dietary lipids from the feeding grounds of a subsidy (Atlantic herring) to the livers of predators in the recipient ecosystem.

Finally, our understanding of the kelp forest ecosystem will improve with empirical tests of hypothesized impacts of cross-ecosystem subsidies, and with the incorporation of trophic subsidies into ecosystem models. Mesocosm (e.g., Yeager et al. 2016) and field experiments (e.g., Polis and Hurd 1996) will give us further insight into how subsidies shape and alter food webs. Efforts to simultaneously quantify subsidy delivery rates and subsidy consumption by kelp forest organisms are essential as we test the true impacts of subsidies across trophic levels and narrow in on subsets of the food web where the largest effects might be observed (Small et al. 2013). Studies in kelp forests, where multiple inputs subsidize a diversity of consumers spanning several trophic levels, may allow researchers to explore the complexity associated with ecological subsidies. Explicit looks at kelp forest species interactions such as competition and predation in the presence and absence of subsidy resources will highlight ecosystem-level impacts. And certainly, matching metrics of subsidy magnitude and timing with long-term ecosystem monitoring data has the potential to bring unexpected effects of subsidies to light.

CROSS-ECOSYSTEM KELP FOREST SUBSIDIES IN A CHANGING OCEAN

In a changing world, the dynamics of subsidies are not static, and future environmental changes to subsidies will have implications for natural communities (Griffiths et al. 2017). Sato et al. (2016) use a field manipulation to conclude that shifts in the timing of a pulsed subsidy to a freshwater stream ecosystem can fundamentally alter the ecosystem-wide impacts of that subsidy. In this experiment, subsidy timing affected consumer growth rates and timing of maturation, population biomass of both cutthroat trout (apex predators) and stream invertebrates (consumers), and nutrient recycling and decomposition rates (Sato et al. 2016). Similarly, there is experimental

evidence that human-caused changes in predator abundance (including the introduction of non-native predators), temperature, and nutrient flux in stream systems impact the magnitude of subsidies, identity of these subsidies, and timing of their delivery (Baxter et al. 2004, Greig et al. 2012). As changes in the temperature, oxygen levels, acidity, and circulation patterns in our coastal oceans continue, connectivity patterns will change, and ecosystem-wide impacts of subsidies will shift. Intensification of seasonal upwelling and/or other changes to upwelling dynamics on the West coast of North America is expected to alter dispersal pathways of larval and juvenile rockfish to the kelp forest ecosystem (Parrish et al. 1981, Bakun 1990, Bakun et al. 2015, Rykaczewski et al. 2015). Because substantial work has been done to understand patterns and processes of the juvenile rockfish subsidy, we can begin to predict how delivery to the kelp forest ecosystem might change into the future. More frequent hypoxic conditions in coastal waters are expected to impact recruitment dynamics of marine invertebrates, many of which are subsidies for nearshore predators (Powers et al. 2001, Chan et al. 2008). Model predictions of range shifts in response to temperature increases in the ocean will shift interaction networks, and geographic patterns of subsidies, with unknown impacts for the importance of subsidies (Perry et al. 2005, Pinsky et al. 2013, Bates et al. 2014). As waters warm, ecologists predict metabolic rate increases in heterotrophs, but are unsure whether ingestion of food will keep pace (Gilbert et al. 2014, Iles 2014). No studies to our knowledge have been done on the role that trophic subsidies will play in allowing consumer ingestion to keep up with the increasing energetic demands of a changing ocean environment. In addition to these bilateral species interactions, there is the potential for impacts to propagate up or down a food web, inducing changes to multi-species interactions. This potential for trophic cascades resulting from subsidy resources has been borne out in both terrestrial and freshwater examples, with some researchers even suggesting that the rates of exogenous inputs might be key to our understanding of why trophic cascade strengths vary across ecosystems (Polis and Hurd 1996, Polis et al. 1997, Nakano et al. 1999, Baxter et al. 2005,

Leroux and Loreau 2008). Finally, as more species move around the world and invade new ecosystems, subsidy dynamics will be impacted. Invasive species can be important trophic subsidies (Quijón et al. 2017).

Following the conceptual framework presented by Larsen et al. (2016) outlining how global change might influence stream riparian subsidy dynamics and consequences, kelp forest ecologists should begin developing questions and studies that explore how changing ocean conditions will affect subsidies, trophic networks and cascades. Global climate change will impact phenology, aspects of metabolism, and the distribution of organisms, creating the possibility for spatial or temporal mismatches between consumers and subsidy delivery (Harley et al. 2006). Future studies should address the pathways and mechanisms by which global change might impact subsidy dynamics.

The topic of ecological connectivity, in the broad sense, has been embraced for its importance in conservation (Carr et al. 2017, Hidalgo et al. 2017). Ecological connectivity impacts many of the processes that shape kelp forest communities, and an understanding of this connectivity is critical for kelp forest management and predicting a system's response to management (Pérez-Matus et al. 2017). For example, genetic connectivity is often used as a source of information to inform fisheries management and conservation decisions. Similarly, practitioners using spatial marine planning tools have long called for a better understanding of ecosystem connectivity and the movement of pelagic larvae and juveniles to adjacent ecosystems. The success of marine protected areas in particular relies on the ability of managers to incorporate ecological connectivity into their design (Carr et al. 2017). However, it is not common for managers to take the cross-ecosystem approach that consideration of trophic ecosystem connectivity necessitates (Loreau and Holt 2004, Massol et al. 2011, Menge et al. 2015). When estimating and measuring connectivity to ensure conservation success, trophic subsidies should not be ignored. Griffiths et al. (2017) look specifically at pelagic–benthic coupling, summarizing mechanisms by which climate change might impact physical processes and the cycling of nutrients, and ecological processes that impact consumer–resource dynamics. They also predict

the directionality of response of subsidy-relevant ecological processes to nutrient loading and fishing, two notable anthropogenic pressures. As adaptive management gains prominence as a conservation tool, ongoing study into the dynamics and variability in trophic subsidies will also be essential (Hidalgo et al. 2017).

Pathways of ocean connectivity and the cross-system flows of subsidy resources are not immune to human-caused disturbances and change. Bishop et al. (2017) review the ways in which sprawl of artificial structures in coastal and marine environments (e.g., marinas, seawalls, offshore energy developments) might be impacting and altering ecosystem connectivity, including the flows of trophic resources. With a meta-analysis of studies using graph theory to describe ecosystem connectivity, Saunders et al. (2015) assess the impact of habitat alteration, human-mediated species movement, overharvesting, and climate change on the presence, strength, and directionality of connectivity. They show that these anthropogenic stressors can impact nodes (i.e., ecosystems or populations in a connected network; in the case of habitat alteration, overharvesting or sea level rise), links (the connection between ecosystems; in the case of species introductions or altered circulation), or both (in the case of climate change).

Expanding our knowledge of the subsidies flowing from the pelagic ocean to nearshore kelp forest systems will provide insights relevant to both terrestrial and other aquatic systems. Though we focus on the kelp forest ecosystem, this is but one example where an improved understanding of the importance of cross-ecosystem subsidies will benefit understanding of ecosystem function and stability. Impacts on trophodynamics are one of the outcomes of connectivity in ecological systems, and a closer look at how the larger process of connectivity works to structure communities should remain a priority (Sheaves 2009). More work is necessary to develop a clear picture of the relative importance of endogenous vs. exogenous productivity in kelp forest and other coastal marine ecosystems. It is clear, however, that trophic subsidies are one of the forces that shape communities and ecosystems. Further research is necessary to determine the direct and indirect effects of trophic subsidies to kelp forests, and to determine the consistency

of these effects among consumers and geographic locations. In addition, questions remain regarding whether subsidies impart stability or destabilize kelp forest communities and predator-prey interactions therein. There are many fruitful avenues of research exploring cross-ecosystem subsidies and their impacts, and inclusion of this important aspect of food web dynamics will surely improve our understanding of kelp forests and other coastal marine ecosystems into the future.

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