2020-2025 Pacific Northwest Dungeness Crab Research Guide

Report Leads: Emily Buckner (Puget Sound Restoration Fund) and Angela Cruz (Washington Sea Grant)
Contributing Authors: Julie Barber (Swinomish Indian Tribal Community, SITC); Katelyn Bosley (Washington Department of Fish and Wildlife, WDFW); Rich Childers (WDFW); Claire Cook (SITC); Sarah Grossman (SITC); Neil Harrington (Jamestown S'Klallam Tribe, JST); Matt Nelson (SITC); Emma Saas (Suquamish Tribe) and Elizabeth Tobin (JST)

Background & Need for Research

Dungeness crab (*Metacarcinus magister)* are decapod crustaceans that inhabit coastal and estuarine waters ranging from the Pribilof Islands, AK to Baja, Mexico (Hart 1984, Jensen & Armstrong 1987). Throughout its range, Dungeness crab serve as the backbone to many West Coast communities who rely on the species due to their cultural, ecological, and economic importance. For example, the Dungeness crab fishery is one of the highest valued and heaviest exploited along the West Coast. In Washington alone, the non-tribal commercial harvest of this species brings in an annual ex-vessel value around $70m USD (Puget Sound and coastal fisheries combined; WDFW unpub. data, 2021) and an average of 220,434 recreational licenses are sold per year (Puget Sound Partnership Vital Signs); this supports many local communities and a global seafood industry. Despite its importance for both tribal and non-tribal communities of the eastern Pacific Coast, many questions regarding how Dungeness crab populations vary and interact with the ecosystem remain unanswered. These significant gaps in our understanding have become particularly evident as harvest in some historically productive areas has declined[11], raising questions regarding the status of *M. magiste*r populations and the sustainability of harvest. In addition to questions of sustainability, it is unclear how vulnerable the species and fishery are to changing climate and ocean conditions (Froehlich et al. 2017). Given these concerns, there is a need for an immediate and coordinated response to fill essential data gaps to better inform the management of this species.

Dungeness Crab Biology & Ecology

---

[1] Prior to 2015, total Dungeness crab harvest in the southern portion of Puget Sound (Crab Regions 6 and 7) averaged 364,000 lbs. (~165,000 kg) annually (WDFW, unpub. data, 2021). By 2018, harvest dropped below 45,000 lbs. (~20,400 kg) prompting closure of the fisheries in those regions. Since that time, crab populations in Regions 6 and 7 have not recovered. The crab fishery has remained closed in Region 7 and only a very limited fishery has been permitted in Region 6 (WDFW, unpub. data, 2021).

Dungeness crab have multiple developmental stages which occupy distinct habitats throughout their lifecycle (Lough 1975, Methot 1989). Beginning as planktonic larvae, newly hatched Dungeness crab are released into the water column, where they progress through five zoeal and one megalopal stage over a period of four months (ranging from 115 days in California to 154 days in Alaska) before transitioning to benthic habitats as juveniles (Rasmuson 2013). Larval Dungeness crab are strong swimmers, occupying surface waters during the early evening/night and at depth during daylight hours (Jamieson & Phillips 1993). Juvenile crab (instars) preferentially settle in structurally complex intertidal and shallow subtidal habitats (McMillan et al. 1995, Galloway & Shanks 2017). Young-of-the-year juvenile instars rear in these protective habitats for six to 12 months, before migrating to deeper habitats (Dinnel et al. 1987, Armstrong et al. 1989). Dungeness crab reach sexual maturity around two years of age (up to five years for slower growing populations). Females carry between 1.5 and 2.5 million eggs, which hatch between December and June (as reviewed in Rasmuson 2013).

Adult and juvenile Dungeness crab are opportunistic feeders in both estuarine and subtidal habitats, feeding on bivalves, fishes, shrimp, and other crabs (Stevens et al. 1982, Lawton & Elner 1985, Jensen & Asplen 1998). Juvenile crab are often eaten by demersal fishes like flounder, sole, and sculpin (Armstrong et al. 1995, 2003), as well as shore crabs and the introduced European green crab (*Carcinus maenas*) (McDonald et al. 2001). Dungeness crab often travel great distances to feed, balancing food resource availability against predation risks (Holsman et al. 2006). Adult Dungeness crab have few predators, but are known to be eaten by lingcod, cabezon, wolf eels, octopuses, and sea otters (Reilly 1983, Garshelis et al. 1986). In addition to predation, other threats to the species include hypoxia (low oxygen content) (Bernatis et al. 2007, McGaw 2008, Chan et al. 2019), ocean warming and acidification (McConnaughey et al. 1995, Sulkin et al. 1996, Bednaršek et al. 2020), sedimentation particularly due to dredging (Chang & Levings 1978, Armstrong et al. 1987), and vulnerability of larvae to disease, pesticides, and other pollutants (e.g., metals) (Buchanan et al. 1970, Armstrong, Buchanan, & Caldwell 1976, Armstrong, Buchanan, Mallon, et al. 1976, Fisher & Nelson 1977, Caldwell et al. 1978, Martin et al. 1981).

Photo caption: Dungeness crab at several life stages (left to right): megalopal (two different cohorts shown), juvenile instar, and adult. All photos taken in Puget Sound, WA by the Swinomish Indian Tribal Community.

Although the biology and ecology of Dungeness crab is relatively well-understood compared to other marine invertebrates, fundamental gaps still exist, notably in crab populations within inland waters, such as the Salish Sea. There is currently a lack of information regarding the spatial and temporal distribution of larvae and juvenile settlement, adult migration patterns, genetic population structure, and environmental influences on vulnerable life history stages. Given the unprecedented changes happening to our global environment, it is more important than ever to better understand the biology and ecology of this iconic species. This critical need for research and the collective interest in pursuing collaborative research to address data gaps prompted the formation of the Pacific Northwest Crab Research Group with the goal of pursuing a collaborative approach to generate and share information needed to learn more about the marine environment and ensure a sustainable future for Dungeness crab and the communities that rely on them.

Who We Are

The Pacific Northwest Crab Research Group (PCRG), formed in 2018, is a consortium of scientific research partners, resource managers, and community members looking to address critical research gaps in our knowledge of Dungeness crab. Working with the mission to *promote and support sustainable Dungeness crab populations in the Pacific Northwest*, the aim of PCRG is to bring together scientists and stakeholders from different disciplines and specialties relevant to Dungeness crab to: define and prioritize research questions; identify how PCRG can best tailor its research to inform resource managers; and share research results from PCRG activities. As a collective network, the goals of PCRG are to pursue <u>collaborative research</u> to:

1. Monitor crab populations and develop tools to forecast crab abundance;
2. Better understand and sustain the ecological role of crab; and
3. Produce information addressing multiple critical data gaps for Dungeness crab.

The group works to implement these goals by developing collaborative projects and by facilitating information and knowledge sharing between members. Projects are funded by a combination of avenues including grants solicited by PCRG as a group and individual project components led by PCRG member teams.

Prioritizing Research

The purpose of this research guide is to document the current research topics/questions identified and prioritized by PCRG regarding Dungeness crab biology and management. Together, management priorities and research questions highlighting knowledge gaps act to direct the research pursued by the group (Fig. 1). Below we identify the top 10 research questions prioritized by PCRG members and discuss how to move towards information-driven action.

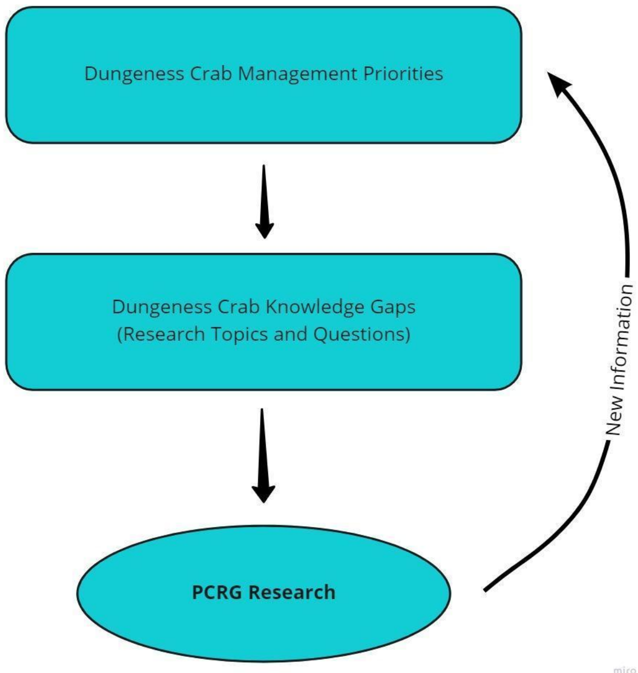

Figure 1. Schematic indicating how PCRG research is determined. Management priorities identify research topics and knowledge gaps, from which research questions can be developed to inform/direct PCRG research efforts. The knowledge derived from those strategic research efforts ultimately integrate into management and can be used to influence new manager priorities.

Management Priorities

The PCRG is not a management entity, and as such, has no decision-making authority over Dungeness crab fisheries. However, PCRG plays a role in supporting fishery managers by providing baseline data that is critical for making informed decisions about the resource. Therefore, in order to pursue research that is the most relevant for informing management, the needs of fishery managers must be considered in the research prioritization and planning phase. During the winter 2020 workshop, PCRG members (including several Washington crab co-managers) identified PCRG's major management topics, as they relate to the Dungeness crab fishery. Through this process, the following six priority management topics were identified: Population Assessment; Spatial and Temporal Management; Adaptive Management; Habitat Conservation and Mitigation; Diseases, Pests, and Pollution; and Fishery Impacts. Participants then ranked these topics in order of relevance and priority for managers and fishery sustainability (Fig. 2). These focal management topics are discussed in detail below.

Note that because of the Washington-specific expertise of group members who participated in PCRG workshops, these topics were primarily determined based on Washington fishery issues, and are described with that geographic focus, though these issues can likely be extrapolated to other regions.

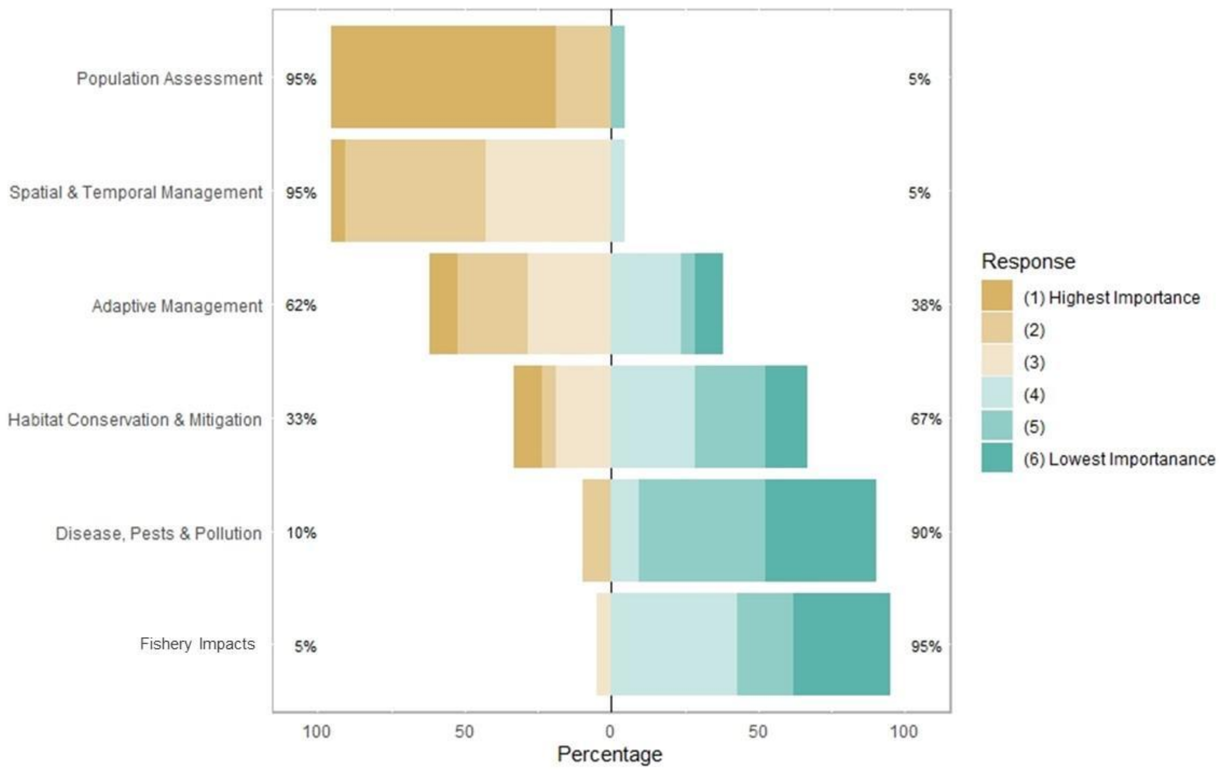

Figure 2. Management topics by order of importance, as determined by PCRG Winter 2020 Workshop participants. It is important to note that lower ranking topics are not lacking in importance. Indeed, there are so many gaps in the literature that research focusing on any of these topics can be used to improve management of the fishery. The higher-ranking topics represent the most pressing topics in light of the lack of current information and management structures.

Population Assessment

Population assessments, or stock assessments, are a tool used to estimate the abundance of a given biological population. These assessments are generally based on an integrated modeling framework which incorporates several data sources to provide an estimate of a species biomass in a given area including fishery harvest data, population structure and life history parameters (i.e., growth rates, sexual maturity, recruitment success, mortality rate; NMFS 2001). Because of their reliance on a wide range of data, these types of assessments are often found to be the most reliable means to estimate the status of fisheries stocks (Branch et al. 2011). Stock assessment outputs not only provide information on stock productivity, they are also important when developing sustainable fishery management practices designed to maximize yield while minimizing the risk of overfishing (NMFS 2001).

Despite its high commercial value, no formal stock assessment exists for Dungeness crab in Washington state. Though the fishing rates are well tracked and recorded, this species' absolute population abundance remains unknown. Currently, the only population abundance information for Dungeness crab comes from fishery landings data and some annual pre- and post-harvest population surveys conducted specifically to assess the availability of legal-sized males. The overall dearth of high-quality and complete life history and abundance data, which are required to construct an accurate population model that encompasses all life history stages, remains the primary challenge in producing a reliable Dungeness crab stock assessment.

The population assessment management topic was ranked as the most important by PCRG members for ensuring the sustainability of the Dungeness crab fishery. Thus, research focused on acquiring data needed to create a population assessment model should be prioritized (see research gaps highlighted under Population Status, Structure and Dynamics).

Spatial & Temporal Management

Spatial and temporal management refers to the scale in which fishery management practices are applied. Spatial management units are typically defined by geographical and/or political boundaries which are often misaligned with the true spatial structure of the harvested resource (Berger et al. 2020). Within a spatial management unit, the applied management procedures typically assume a closed homogeneous population, ignoring heterogeneity in population vital rates and connectivity among adjacent management units (Kerr et al. 2017). In recent years, fishery management practices have evolved to accommodate the need for more refined spatial management through the development of tools to identify complex population structure (e.g., genomics and tagging) and population assessment models that account for stock heterogeneity (Cadrin 2020, Bosley et al. 2021). However, for the Dungeness crab fishery, the temporal and spatial resolution of the data needed to apply these advanced techniques are lacking, therefore the ability to align spatial management practices with true biological population structure remains limited.

Dungeness crab management in Washington’s inland waters is spatially and temporally complex, with many small discrete spatial management units and a protracted fishing season. Fisheries are generally timed to avoid vulnerable life stages of the species to preserve the stock (e.g., closed fishing during the molting period for Dungeness crab). Since the 1940’s the ‘3-S’ management scheme has largely proven effective in maintaining sustainable harvest on the U.S west coast, where harvest is managed (1) with a minimum size limit, (2) by only allowing males to be harvested and (3) by setting seasons to protect soft shelled crab (Richerson et al. 2020). As climate change becomes a more prominent threat to the Dungeness crab fishery, managers are concerned about the resiliency of the ‘3-S’ management scheme under changing ocean conditions. Warming waters may impact molting patterns and growth trajectories which could impede the current management scheme and potentially reduce protection to vulnerable life stages. Therefore, it is essential to have a thorough understanding of Dungeness crab life history and how population vital rates are expected to change across space and through time. High quality population data is needed at spatial and temporal scales that allow managers to assess effectiveness of the current management strategy and management units, identify the time and location of optimal harvest opportunities, and determine when and where to enact conservation measures if needed.

Photo caption: Co-managers for the Washington state Dungeness crab fishery, such as the Department of Fish and Wildlife (WDFW, left) and treaty tribes (right) conduct research to better understand population dynamics. Photo credit: WDFW and Swinomish Indian Tribal Community

Adaptive Management

Adaptive management is an approach to dealing with large uncertainty in a fishery and describes the approach used to respond to problems in real time by having the necessary baseline information about the resource and its environment (Walters 2007). This approach is often colloquialized as “learning by doing”, meaning management needs to be implemented as an experiment and readily adjusted given new data or situations (Halbert 1993). The process of adaptive management is often challenging, requiring planning from the onset to define management questions and acquire adequate baseline data (Reever Morghan et al. 2006).

Fisheries are inherently variable and prone to unexpected shocks and natural cycles with climate change creating even more uncertainty (Cheung et al. 2010, Quentin Grafton 2010). The Dungeness crab fishery is no exception, experiencing fluctuations in harvest from season-to-season (Botsford et al. 1982, Armstrong et al. 2011) and spatial and temporal changes in the population (WDFW unpub. data, 2021). Recent investigations into potential climate change impacts show deleterious effects to larval development when exposed to increasingly acidic ocean conditions (Bednaršek et al. 2020). In order to establish a more resilient and climate-ready fishery in the face of changing ocean conditions, managers need to build a more holistic understanding of Dungeness populations within specific regions (e.g., Puget Sound sub-basins), as well as acquire real-time data on ocean and population conditions. Much of the information necessary for designing and implementing adaptive management frameworks is also required for population assessments and spatial and temporal management.

Habitat Conservation, Restoration, and Mitigation

Habitat conservation, restoration, and mitigation are common management considerations in sustainable fisheries, as a healthy habitat is important for maintaining a robust stock. In order to conserve and restore habitat for Dungeness crab, it is essential to identify critical habitats and quantify use and importance by the species across various life stages. Habitat preference is well documented; juveniles settle in highest abundances in shallow nearshore, estuarine environments with complex three-dimensional habitat, such as oyster shell or eelgrass coverage, while adults are typically found from the intertidal up to 230m depth on sandy-mud bottoms (Holsman et al. 2006; Cleaver 1949; McMillan et al. 1995). What is less well known, particularly within the Salish Sea, is how, when, and why Dungeness crab move between critical habitats, and how conditions such as temperature and salinity impact that behavior (some of these questions were addressed for hypoxia in Froehlich et al. 2013). Understanding the patterns of crab habitat use, and the conditions that may drive those patterns, could assist in the identification of areas where conservation or restoration/mitigation measures would best promote a healthy and resilient Dungeness crab population, particularly in the face of rapidly changing ocean conditions and habitat loss.

In terms of mitigation, Dumbauld et al. (1993) found enhancing habitat with oyster shell increased crab survival. As such, oyster shell additions have been utilized for mitigating the impact of dredging on crab habitat despite later findings suggesting that interspecific competition reduces the effectiveness of this type of mitigation project for Dungeness crab (Visser et al. 2004). While habitat conservation is preferred over restoration or mitigation, future studies investigating human impacts on habitat should consider designing experimental studies such as Dumbauld's (1993), to determine the most appropriate design for mitigation.

Disease, Pests, and Pollution

Disease

Crustacean populations are known to suffer direct and indirect losses from several pathogens but overall mortalities are difficult to estimate. Mortalities are the most striking feature of an epizootic, but other disease effects such as reduced growth, fecundity, and loss of product quality can greatly impact populations that are commercially exploited (Morado & Sparks 1988).

Microsporidians are among the most common and most pathogenic of crustacean disease agents, and are especially well documented among the decapods (Couch 1983; Sindermann 1990; Sparks 1985). The number of known microsporidian species is now about 800 (Canning 1990), with over 140 species described from crustacean hosts (Couch 1983). There are very few diseases described in Dungeness crabs (Meyers et al. 1985) and only three protozoan infections have been reported: a systemic ciliate disease caused by *Paranophrys* sp. (Sparks et al. 1982; Armstrong et al. 1981), an undescribed microsporidian that infects muscle tissue (Morado & Sparks 1988), and *Nadelspora canceri*, a microsporidian that has unusual needle-shaped spores that are easily recognized when muscle is viewed under a light microscope (Olson et al. 1994). *Paranophrys* sp. requires entry into the crab through injury of the exoskeleton and causes destruction and dysfunction of major organ systems and ultimately death of the host (Sparks et al. 1982). No detailed information exists on the microsporidian that was observed infecting Dungeness crabs by Morado and Sparks (1988) except that spores were oval-shaped and not contained within membranes, suggesting the parasite belongs in the family Nosematidae.

Nadelspora canceri infects the striated muscle in the Dungeness crab host and parasite spores are found in vast numbers in the muscle tissue. In heavy infections, the muscle appears to be virtually replaced by spores. Disease survey in the early 1990's found *Nadelspora canceri* infections in Dungeness crab along the U.S. Pacific Coast from Bodega Bay, California, to Grays Harbor, Washington, with prevalence lowest in open oceans (0.3%) and highest in estuaries (usually about 14% but up to 41% in one location) (Childers et al. 1996). Extensive surveys of Dungeness crab for *N. canceri* infection north of Grays Harbor, including Puget Sound, have not found any infected crab north of Grays Harbor (R. K. Childers Personal Communication 2021). *Nadelspora canceri* infections are lethal to the crab host (R. K. Childers Personal Communication) but impacts to the crab populations from the disease are unknown. To monitor the northward spread of *Nadelspora*, fishery managers and researchers conducting crab population surveys in the Salish Sea could incorporate visual inspections of crab for *Nadelspora* infections as a component to the population surveys.

Pests

One of the major 'pests' of concern for Dungeness crab in the Pacific Northwest is the European green crab (*Carcinus maenas*), an invasive species whose presence along the West Coast has been documented and increasing since 1989 (Grason et al. 2018, Mueller & Jefferson 2019). In Washington state, dedicated monitoring efforts have found limited numbers of green crab in inland waters, though a few locations consistently report very high numbers (Grason et al. 2018, Mueller & Jefferson 2019). While the full potential of a green crab invasion, and its impacts on native Dungeness crab populations, has not yet been realized in Washington state, evidence from other regions point to the potential for an established green crab population to have severe consequences. For example, it is likely that green crab could decimate critical Dungeness crab habitat due to their digging and burrowing behavior (Jamieson et al. 1998, Hoagland & Jin 2006); or impact Dungeness crab prey availability by consuming much of the local clam populations (e.g., Whitlow 2009). Improving our understanding of the potential ecological impacts of an invasion would help managers better prepare for a future with green crab established in the region.

Pollution

Decreased water quality is a stressor for Dungeness crab with ramifications for the fishery, whether via direct anthropogenic inputs such as pesticides and trace metals (Caldwell 1977), the presence of biotoxins (Ekstrom et al. 2020), or low oxygen or acidic conditions (Bednaršek et al. 2020, Berger et al. 2021). For example, recreational and commercial harvests may be closed or delayed due to recommendations from state health departments monitoring for domoic acid, a biotoxin produced by a species of algae that temporarily accumulates in crab tissue and can cause severe illness in humans if consumed ('Domoic Acid', WDFW). Hypoxia (low oxygen) and ocean acidification are known to increase mortality in adult and larval crab, respectively (Chan et al. 2008, Miller et al. 2016), but the significance of the impacts of these 'pollutants' on Dungeness crab population dynamics is unclear. Since models show the West Coast as one of the most vulnerable regions to ocean acidification in the United States, and monitoring shows that hypoxic conditions are increasing, these issues are quickly becoming a priority consideration for managers, though a challenging one (Billé et al. 2013; Ekstrom et al. 2015; Klinger et al. 2017, NCCOS Project Report). In order to protect human health and promote population sustainability, it is essential to uncover when and where different types of 'pollution' hotspots occur. This hotspot identification would allow managers to better plan and coordinate harvests and potentially identify crucial habitat refuges for local crab populations that may be key for population resilience (Kapsenberg & Cyronak 2019; Berger et al. 2021).

Photo caption: Local commercial crabbers are important collaborators in research and can fill knowledge gaps with local and traditional insight. Photos by Jim Gibson and Swinomish Indian Tribal Community.

Fishery Impacts

To reduce risk of overexploitation, a persistent challenge of managing capture fisheries is assessing and accounting for fisheries-related impacts such as mortality and/or injury (Juanes & Smith 1995, Uhlmann & Broadhurst 2015). Developing a better understanding of how current management strategies impact Dungeness crab populations can assist with identifying ways to minimize potential harvesting impacts on the exploited population. Fisheries-related mortality can include loss due to entrainment in derelict gear, detrimental handling of organisms, and poaching (Breen 1987, Antonelis et al. 2011). Of particular interest is the fact that ~12,000 traps are lost annually in Washington's inland waters (Antonelis et al. 2011). These lost traps lead to an estimated annual mortality of 170,000 legal-sized male crab, indicating a strong need for the removal of lost traps (Antonelis et al. 2011). Additionally, harvest of one sex, as is done under 3-S managment, can cause shifts in sex-ratios or can impact the genetic structure of a population (Allendorf et al. 2008, Ogburn 2019). While some research on Dungeness crab reproductive output suggests that >80 % of females can mate successfully despite the exploitation of males (Dunn & Shanks 2012, Rasmuson 2013, Ogburn 2019), we would benefit from an increased understanding of how reproductive output, sperm storage, and fertilization processes are affected by the fishing impacts and the 3-S management strategy, particularly in the Salish Sea.

Research has also shown that injury in crabs can have negative effects on individual fitness, which is especially important when studying sublegal animals that are released upon trap retrieval (Juanes & Hartwick 1990, Juanes & Smith 1995, Barber & Cobb 2007). The Dungeness crab fishery in Washington's Salish Sea is currently managed to avoid harvest during molting, when crab shells are soft and most vulnerable to handling (Kruse et al. 1994). Yet, the ecological drivers of molt timing are not well understood, leaving managers unable to anticipate the ideal timing for fishery closures as it relates to shell condition. We also do not completely understand the impact of capture or injury on ovigerous female Dungeness crabs despite the fact some crustacean species are known to mutilate their egg masses upon capture (Darnell et al. 2010). Thus, research considering factors that influence molting and injury to both male and female crab will be beneficial for improving future management strategies for Dungeness crab.

Research Topics

Critical knowledge gaps regarding Dungeness crab can be categorized into four general research topics: Population Status, Structure, and Dynamics; Land Use and Climate Change Impacts; Fishery and Industry Impacts; and Ecology and Food Web Dynamics (defined below).

The research questions contained herein reflect how to address the PCRG-identified knowledge gaps within each category (Boxes 1 to 4), determined during the winter 2020 workshop. During this workshop, PCRG members were also asked to rank the priority of the research topics (Fig. 3). Note that the majority of workshop participants were scientists and managers who work within the Salish Sea and, as such, identified gaps in knowledge for that region specifically. Some of these knowledge gaps may have been explored previously in other parts of the Pacific Northwest (e.g., outer WA and OR coast, AK, BC).

- Population Status, Structure, and Dynamics (Box 1) - this category includes questions related to Dungeness crab populations and the biological information necessary for best determining crab abundance.

- Land Use and Climate Change Impacts (Box 2) - this category aims to address how changing environmental conditions and land use practices may impact future Dungeness crab populations.

- Fishery and Industry Impacts (Box 3) - this category focuses on the interactions between fishery and industry practices and Dungeness crab populations.

- Ecology and Food Web Dynamics (Box 4) - this category includes questions about the interactions between Dungeness crab, their environment, and other species.

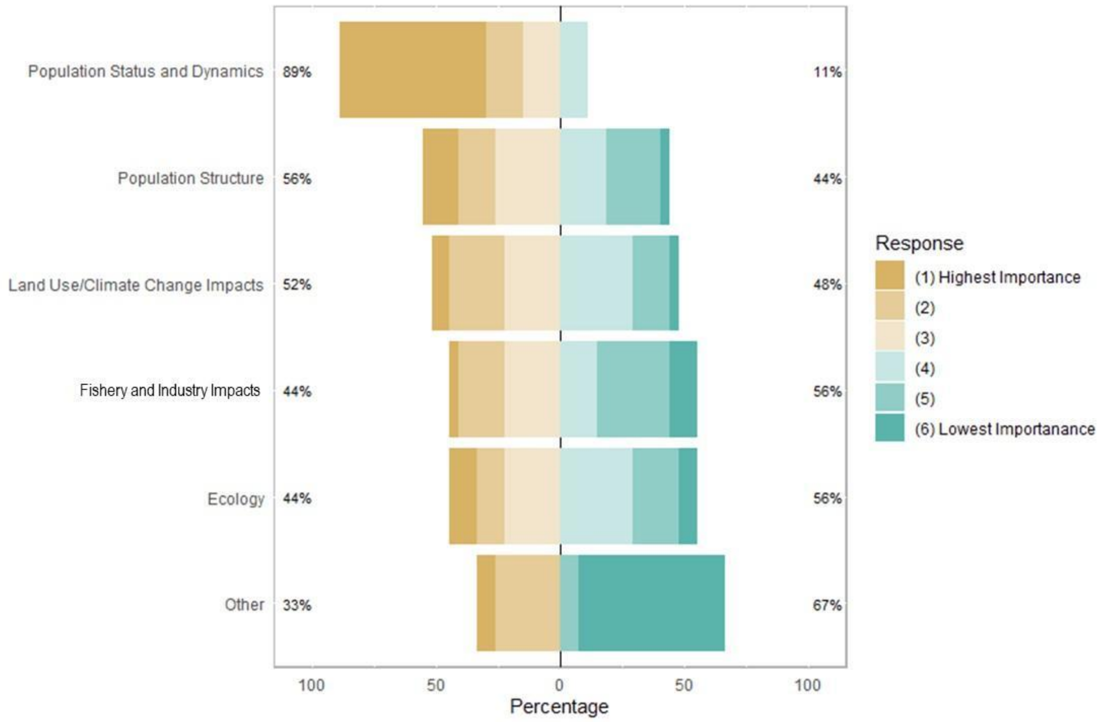

Figure 3. PCRG member ranking of research areas identified in January 2020. Note that population status and dynamics was combined with population structure after the ranking was complete.

The boxes below contain PCRG member questions, organized by research area. Members collectively gathered questions that, once answered, would be useful in filling important knowledge gaps. PCRG members simultaneously ranked their top research question choices across all research areas, the 10 highest ranked are identified below:

Top 10 PCRG Research Questions

- What are the best cost-effective and robust predictors of adult Dungeness crab abundance?
- How does larval abundance correlate to adult crab abundance in a given area?
- What are the population bottlenecks (e.g., spatial, temporal, life history stage)?
- What are the source and sink dynamics along the West Coast for Dungeness crab populations?
- What biological metrics are needed to develop accurate stock assessments for Dungeness crab?
- What are the effects of climate change on each of the Dungeness crab life history phases?
- How will climate change affect different types of management strategies?
- What amendments to the 3-S management framework can we test using a management strategy evaluation (e.g., size limits, timing to avoid molting, etc.)?
- What are the top-down vs. bottom-up impacts on Dungeness crab populations?
- What are the impacts of environmental stressors on various life history phases?

Box 1. Population Status, Structure, and Dynamics
● What are the best cost-effective and robust predictors of adult Dungeness crab abundance? ● How does larval abundance correlate to adult crab abundance in a given area? ● What are the population bottlenecks (e.g., spatial, temporal, life history stage)? ● What are the source and sink dynamics along the West Coast for Dungeness crab populations? ● What biological metrics are needed to develop accurate stock assessments for Dungeness crab? ● What is the natural mortality rate of Dungeness crab? ● How can we use test fishery data in a predictive way? ● Are management areas appropriate for the population distribution? ● What are the mechanisms and extent of larval transport and distribution? ● Can we characterize the spatio-temporal variations in molting and mating patterns? ● How many populations of Dungeness crab exist throughout their range? ● What is the impact of a skewed sex ratio in the population? ● What is the connectivity of regional populations of Dungeness crab? ● What is the optimal size-frequency distribution for a sustainable fishery? ● Does the population structure change across space and through time? ● What are the migration patterns of adult Dungeness crab within and between regions? ● Can we use alternative methods for assessing population age structure? ● What is the best indicator of mating success?

Box 2. Land Use and Climate Change Impacts
● What are the effects of climate change on each of the Dungeness crab life history phases? ● How will climate change affect different types of management strategies? ● How will changes in sea surface temperature affect population dynamics? ● What are the fisheries-related socio-economic impacts associated with climate change? ● Will there be shifts in population distribution as oceanic conditions change? ● How does shoreline development and use impact population dynamics? ● What are the interactions between climate change, harmful algal blooms, and the Dungeness crab fishery? ● Is estuarine restoration a valid tool for promoting resilience in Dungeness crab? ● How do anthropogenic stressors affect Dungeness crab populations?

Box 3. Fishery and Industry Impacts
● What amendments to the 3-S management framework can we test using a management strategy evaluation (MSE) (e.g., size limits, timing to avoid molting, etc.)? ● What are the effects of fishing during mating or molting seasons? ● How do management strategies influence socio-economic factors or vice versa?

- What socio-economic factors would be best utilized in a management strategy evaluation?
- What are the effects of biotoxins on the crab fishery?
- How does derelict gear impact crab populations?
- How does the act of handling crab during a fishery impact crab survival?
- What are the potential effects of skewing the sex ratio in a male-only fishery?
- What are the spatial-temporal variations in unreported catch?

Box 4. Ecology and Food Web Dynamics

- What are the top-down vs. bottom-up impacts on Dungeness crab populations?
- What are the impacts of environmental stressors on various life history phases?
- How do environmental factors influence growth rates for Dungeness crab?
- How do the bioenergetics of Dungeness crab differ throughout their range?
- Do non-native eelgrass beds provide the same nursery habitat function as native eelgrass beds for Dungeness crab?
- What are the impacts of predators (otter, octopus, lingcod, etc.) on Dungeness crab?
- How do diseases impact Dungeness crab across space and through time?
- How will changes in phytoplankton community assemblages impact Dungeness crab survival?
- What are the temporal and spatial patterns of habitat use of juvenile Dungeness crab and do they differ by region?
- Which species utilize Dungeness crab as a critical food source?
- What role do Dungeness crab play in marine food webs as a prey item?

Charting a Path to Information-Directed Action

Since its inception in 2018, PCRG has worked to build relationships by reaching out and connecting with partners interested in advancing our mission. Over the last few years we have grown to an organization with nearly 100 members, many of whom have shared their expertise and worked to identify knowledge gaps. This process has ultimately assisted PCRG by helping us target specific management priorities and determine where to focus research efforts during our first five years as a program.

Photo Caption: PCRG light trap monitoring for larval Dungeness crab with commercial fishing boat in background. Shaw Island, WA. Photo by Emily Buckner.

Moving forward, we hope this research guide will provide a foundation upon which we can advance collaboration and build even more targeted and effective research plans. This document not only guides PCRG and its individual members in their research, but also serves as a resource for the greater scientific community working to address high priority research areas for Dungeness crab. While some specific PCRG research projects are already underway (Appendix 1), the myriad of unanswered research questions is large enough that researchers will benefit from a coordinated effort to continually update top priority needs. As such, the knowledge gaps and management priorities in this guide will be regularly revisited by the PCRG and updated, as necessary, every five years.

Although PCRG research programs are still relatively young, we believe it is prudent to continue to develop our capacity to coordinate research efforts, build upon or create new and sustainable research programs, and determine the best approaches for communicating our science to diverse audiences. We suggest that during the development of the next research guide in 2026, we build off of lessons learned during our inaugural five years and explore various future scenarios for the continual improvement of our guided and collaborative research program.

Table 1. Summary of current/pending PCRG research projects and what questions they address.

Project Title	**Years Implemented**	**Research Question(s) Addressed**
Larval Crab Monitoring (WA & BC)	2019-present	● What are the best cost-effective and robust predictors of adult Dungeness crab abundance? ● How does larval abundance correlate to adult crab abundance in a given area? ● What are the population bottlenecks (e.g., spatial, temporal, life history stage)? ● What are the source and sink dynamics along the West Coast for Dungeness crab populations?
Characterizing population connectivity of Dungeness crab in Puget Sound (Puget Sound)	2021-present	● What is the connectivity of regional populations of Dungeness crab? ● How many populations of Dungeness crab exist throughout their range? ● What are the source and sink dynamics along the West Coast for Dungeness crab populations?
Fishery Independent Survey (WA)	In development	● What biological metrics are needed to develop accurate stock assessments for Dungeness crab? ● What is the impact of a skewed sex ratio in the population? ● Does the population structure change over time by region?

		• Can we characterize the spatio-temporal variations in molting and mating patterns? • Does the population structure change across space and through time? • What are the migration patterns of adult Dungeness crab within and between regions? • How can we use test fishery data in a predictive way? • Are management areas appropriate for the population distribution?

Preferred Citation

Buckner, E., A. Cruz, J. S. Barber, K. Bosley, R. Childers, C. Cook, S. Grossman, N. Harrington, M. Nelson, E. Saas and E. Tobin. 2022. 2020-2025 Pacific Northwest Dungeness crab research guide. Pacific Northwest Crab Research Group.

Literature Cited

Allendorf, F.W., P.R. England, G. Luikart, P.A. Ritchie & N. Ryman. 2008. Genetic effects of harvest on wild animal populations. *Trends Ecol. Evol.* 23:327–337.

Antonelis, K., D. Huppert, D. Velasquez & J. June. 2011. Dungeness crab mortality due to lost traps and a cost–benefit analysis of trap removal in Washington state waters of the Salish Sea. *North American J. Fish. Manage.* 31:880–893.

Armstrong, D., L. Botsford & G. Jamieson. 1989. Ecology and population dynamics of juvenile Dungeness crab in Grays Harbor estuary and adjacent nearshore waters of the southern Washington coast. Report to the U.S. Army Corps of Engineers, U.S. Army Corps of Engineers, Seattle, Washington.

Armstrong, D.A., D.V. Buchanan & R.S. Caldwell. 1976. A mycosis caused by *Lagenidium sp*. in laboratory-reared larvae of the Dungeness crab, *Cancer magister*, and possible chemical treatments. *Journal of Invertebrate Pathology* 28:329–336.

Armstrong, D.A., D.V. Buchanan, M.H. Mallon, R.S. Caldwell & R.E. Millemann. 1976. Toxicity of the insecticide methoxychlor to the Dungeness crab *Cancer magister*. *Mar. Biol.* 38:239–252.

Armstrong, D.A., E.M. Burreson & A.K. Sparks. 1981. A ciliate infection (*Paranophrys sp*.) in laboratory held Dungeness crabs, *Cancer magister*. *Journal of invertebrate pathology* 37:201–209.

Armstrong, D.A., P.S. McDonald, G.H. Kruse, A.H. Hines & J.M. Orensanz. 2011. A crab for all seasons: the confluence of fisheries and climate as drivers of crab abundance and distribution. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram & D. Woodby, editors. Biology and management of exploited crab populations under climate change. University of Alaska Fairbanks: Alaska Sea Grant. pp. 1–47.

Armstrong, D.A., C. Rooper & D. Gunderson. 2003. Estuarine production of juvenile Dungeness crab (*Cancer magister*) and contribution to the Oregon-Washington coastal fishery. *Estuaries* 26:1174–1188.

Armstrong, D.A., T.C. Wainwright, J. Orensanz, P.A. Dinnel & B.R. Dumbauld. 1987. Model of dredging impact on Dungeness crab in Grays Harbor, Washington. Fisheries Research Institute - University of Washington, Seattle, Washington.

Armstrong, J.L., D.A. Armstrong & S.B. Matthews. 1995. Food habits of estuarine staghorn sculpin, *Leptocottus armatus*, with focus on consumption of juvenile Dungeness crab, *Cancer magister*. *Fishery Bulletin (Washington, D.C.: 1971)* 456–470.

Barber, J.S. & J.S. Cobb. 2007. Injury in trapped Dungeness crabs (*Cancer magister*). *ICES J. Mar. Sci* 64:464–472.

Bednaršek, N., R.A. Feely, M.W. Beck, S.R. Alin, S.A. Siedlecki, P. Calosi, E.L. Norton, C. Saenger, J. Štrus, D. Greeley, N.P. Nezlin, M. Roethler & J.I. Spicer. 2020. Exoskeleton dissolution with mechanoreceptor damage in larval Dungeness crab related to severity of present-day ocean acidification vertical gradients. *Sci. Total Environ.* 716:136610.

Bednaršek, N., G. Pelletier, A. Ahmed & R.A. Feely. 2020. Chemical exposure due to anthropogenic ocean acidification increases risks for estuarine calcifiers in the Salish Sea: biogeochemical model scenarios. *Front. Mar. Sci.* 7.

Berger, A.M., J.J. Deroba, K.M. Bosley, D.R. Goethel, B.J. Langseth, A.M. Schueller & D.H. Hanselman. 2020. Incoherent dimensionality in fisheries management: consequences of misaligned stock assessment and population boundaries. *ICES J. Mar. Sci*.

Berger, H.M., S.A. Siedlecki, C.M. Matassa, S.R. Alin, I.C. Kaplan, E.E. Hodgson, D.J. Pilcher, E.L. Norton & J.A. Newton. 2021. Seasonality and life history complexity determine vulnerability of Dungeness crab to multiple climate stressors. *AGU Advances* 2.

Bernatis, J.L., S.L. Gerstenberger & I.J. McGaw. 2007. Behavioural responses of the Dungeness crab, *Cancer magister*, during feeding and digestion in hypoxic conditions. *Mar. Biol.* 150:941–951.

Billé, R., R. Kelly, A. Biastoch, E. Harrould-Kolieb, D. Herr, F. Joos, K. Kroeker, D. Laffoley, A. Oschlies & J.- P. Gattuso. 2013. Taking action against ocean acidification: A review of management and policy options. *Environ. Manage.* 52:761–779.

Bosley, K.M., A.M. Schueller, D.R. Goethel, D.H. Hanselman, K.H. Fenske, A.M. Berger, J.J. Deroba & B.J. Langseth. 2021. Finding the perfect mismatch: Evaluating misspecification of population structure within spatially explicit integrated population models. *Fish Fish.*

Botsford, L.W., R.D. Methot & J.E. Wilen. 1982. Cyclic covariation in the California king salmon, *Oncorhyncus tshawytscha*, silver salmon, *O. kisutch*, and Dungeness crab, *Cancer magister*, fisheries. *Fish. Bull. (Washington, D.C.: 1971)* 80:791–801.

Branch, T.A., O.P. Jensen, D. Ricard, Y. Ye & R. Hilborn. 2011. Contrasting global trends in marine fishery status obtained from catches and from stock assessments. *Conserv. Biol.* 25:777–786.

Breen, P.A. 1987. Mortality of Dungeness crabs caused by lost traps in the Fraser River estuary, British Columbia. *North American Journal of Fisheries Management* 7:429–435.

Buchanan, D.V., R.E. Millemann & N.E. Stewart. 1970. Effects of the insecticide sevin on various stages of the Dungeness crab, *Cancer magister*. *J. Fish. Res. Board Can.* 27:93–104.

Cadrin, S.X. 2020. Defining spatial structure for fishery stock assessment. *Fish. Res.* 221:105397.

Caldwell, R.S., D.A. Armstrong, D.V. Buchanan, M.H. Mallon & R.E. Millemann. 1978. Toxicity of the fungicide captan to the Dungeness crab *Cancer magister*. *Mar. Biol.* 48:11–17.

Caldwell, R.S., D.V. Buchanan, D.A. Armstrong, M.H. Mallon & R.E. Millemann. 1979. Toxicity of the herbicides 2,4-D, DEF, propanil and trifluralin to the Dungeness crab, *Cancer magister*. *Arch Environ Contam Toxicol* 8:383–396.

Caldwell, R.S. 1977. Biological effects of pesticides on the Dungeness crab. No. EPA-600/3-77-131, Environmental Research Laboratory.

Canning, E.U. 1990. Phylum Microspora. In: L. Margulis, J.O. Corliss, M. Melkonian & D.J. Chapman, editors. Handbook of Protoctista. Boston: Jones and Bartlett. pp. 53–72.

Chang, B.D. & C.D. Levings. 1978. Effects of burial on the heart cockle *Clinocardium nuttallii* and the Dungeness crab *Cancer magister*. *Estuarine and Coastal Marine Science* 7:409–412.

Chan, F., J.A. Barth, K.K. Kroeker, J. Lubchenco & B. Menge. 2019. The dynamics and impact of ocean acidification and hypoxia: Insights from sustained investigations in the northern California current large marine ecosystem. *Oceanography* 32:62–71.

Chan, F., J.A. Barth, J. Lubchenco, A. Kirincich, H. Weeks, W.T. Peterson & B.A. Menge. 2008. Emergence of anoxia in the California current large marine ecosystem. *Science* 319:920.

Cheung, W.W.L., V.W.Y. Lam, J.L. Sarmiento, K. Kearney, R.E.G. Watson, D. Zeller & D. Pauly. 2010. Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Glob. Chang. Biol.* 16:24–35.

Childers, R.K., P.W. Reno & R.E. Olson. 1996. Prevalence and geographic range of *Nadelspor canceri* (Microspora) in Dungeness crab *Cancer magister*. *Dis Aquat Org* 24:135–142.

Cleaver, F.C. 1949. Preliminary results of the coastal crab (*Cancer magister*) investigation. No. Biological Report No. 49A, Washington State Department of Fish and Wildlife.

Couch, J.A. 1983. Diseases caused by protozoa. In: The Biology of Crustacea. Elsevier. pp. 79–111.

Darnell, M.Z., K.M. Darnell, R.E. McDowell & D. Rittschof. 2010. Postcapture survival and future reproductive potential of ovigerous blue crabs *Callinectes sapidus* caught in the central North Carolina pot fishery. *Trans. Am. Fish. Soc.* 139:1677–1687.

Dinnel, P.A., R.O. McMillan, D.A. Armstrong, T.C. Wainwright, A.J. Whiley, R. Burge & R. Baumgarner. 1987. Padilla Bay Dungeness crab, *Cancer magister*, habitat study. Final Report, U.S. Department of Commerce National Oceanic and Atmospheric Administration, Washington D.C.

Dumbauld, B.R., D.A. Armstrong & T.L. McDonald. 1993. Use of oyster shell to enhance intertidal habitat and mitigate loss of Dungeness crab (*Cancer magister*) caused by dredging. *Can. J. Fish. Aquat. Sci.* 50:381–390.

Dunn, P.H. & A.L. Shanks. 2012. Mating Success of Female Dungeness Crabs (*Cancer magister*) in Oregon Coastal Waters. *J. Shellfish Res.* 31:835–839.

Ekstrom, J.A., S.K. Moore & T. Klinger. 2020. Examining harmful algal blooms through a disaster risk management lens: A case study of the 2015 U.S. West Coast domoic acid event. *Harmful Algae* 94:101740.

Ekstrom, J.A., L. Suatoni, S.R. Cooley, L.H. Pendleton, G.G. Waldbusser, J.E. Cinner, J. Ritter, C. Langdon, R. van Hooidonk, D. Gledhill, K. Wellman, M.W. Beck, L.M. Brander, D. Rittschof, C. Doherty, P.E.T. Edwards & R. Portela. 2015. Vulnerability and adaptation of US shellfisheries to ocean acidification. *Nat. Clim. Chang.* 5:207–214.

Fisher, W.S. & R.T. Nelson. 1977. Therapeutic treatment for epibiotic fouling on Dungeness crab (*Cancer magister*) larvae reared in the laboratory. *J. Fish. Res. Bd. Can.* 34:432–436.

Froehlich, H.E., T.E. Essington, A.H. Beaudreau & P.S. Levin. 2013. Movement patterns and distributional shifts of Dungeness crab (*Metacarcinus magister*) and English sole (*Parophrys vetulus*) during seasonal hypoxia. *Estuaries Coast.* 37:449–460.

Froehlich, H.E., T.E. Essington & P.S. McDonald. 2017. When does hypoxia affect management performance of a fishery? A management strategy evaluation of Dungeness crab (*Metacarcinus magister*) fisheries in Hood Canal, Washington, USA. *Can. J. Fish. Aquat. Sci.* 74:922–932.

Galloway, A. & A. Shanks. 2017. Opening the black box of coastal crab life history: observation of an exceptionally high-density settlement event. *Bull. Eco. Soc. Amer.* 98:236–239.

Garshelis, D.L., J.A. Garshelis & A.T. Kimker. 1986. Sea otter time budgets and prey relationships in Alaska. *J. Wildl. Manage.* 50:637–647.

Grason, E., S. McDonald, J. Adams, K. Litle, J. Apple & A. Pleus. 2018. Citizen science program detects range expansion of the globally invasive European green crab in Washington State (USA). *MBI* 9:39– 47.

Halbert, C.L. 1993. How adaptive is adaptive management? Implementing adaptive management in Washington State and British Columbia. *Rev. Fish. Sci.* 1:261–283.

Hart, J. 1984. Crabs and their relatives of British Columbia. British Columbia Provincial Museum Handbook 40. Victoria, British Columbia Canada: British Columbia Provincial Museum.

Hoagland, P. & D. Jin. 2006. Science and economics in the management of an invasive species. *Bioscience* 56:931–935.

Holsman, K.K., P.S. McDonald & D.A. Armstrong. 2006. Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. *Mar. Ecol. Prog. Ser.* 308:183-195.

Jamieson, G.S., E.D. Grosholz, D.A. Armstrong & R.W. Elner. 1998. Potential ecological implications from the introduction of the European green crab, *Carcinus maenas* (Linneaus), to British Columbia, Canada, and Washington, USA. *J. Nat. Hist* 32:1587–1598.

Jamieson, G.S. & A. Phillips. 1993. Megalopal spatial distribution and stock separation in Dungeness crab (*Cancer magister*). *Can. J. Fish. Aquat. Sci.* 50:416–429.

Jensen, G.C. & D.A. Armstrong. 1987. Range extensions of some Northeastern Pacific Decapoda. *Crustaceana* 52:215–217.

Jensen, G.C. & M.K. Asplen. 1998. Omnivory in the diet of juvenile Dungeness crab, *Cancer magister* Dana. *J. Exp. Mar. Biol. Ecol.* 226:175–182.

Juanes, F. & E.B. Hartwick. 1990. Prey size selection in Dungeness crabs: the effect of claw damage. *Ecology* 2:744–758.

Juanes, F. & L.D. Smith. 1995. The ecological consequences of limb damage and loss in decapod crustaceans: a review and prospectus. *J. Exp. Mar. Biol. Ecol.* 193:197–223.

Kapsenberg, L. & T. Cyronak. 2019. Ocean acidification refugia in variable environments. *Glob. Chang. Biol.*

Kerr, L.A., N.T. Hintzen, S.X. Cadrin, L.W. Clausen, M. Dickey-Collas, D.R. Goethel, E.M.C. Hatfield, J.P. Kritzer & R.D.M. Nash. 2017. Lessons learned from practical approaches to reconcile mismatches between biological population structure and stock units of marine fish. *ICES J. Mar. Sci* 74:1708– 1722.

Klinger, T., E.A. Chornesky, E.A. Whiteman, F. Chan, J.L. Largier & W.W. Wakefield. 2017. Using integrated, ecosystem-level management to address intensifying ocean acidification and hypoxia in the California Current large marine ecosystem. *Elem Sci Anth* 5:16.

Kruse, G., D. Hicks & M. Murphy. 1994. Handling increases mortality of softshell Dungeness crabs returned to the sea. *Alaska Fish. Res. Bull.* 1:1–9.

Lawton, P. & R.W. Elner. 1985. Feeding in relation to morphometrics within the genus *Cancer*: Evolutionary and ecological considerations. *In Proceedings of the symposium on Dungeness crab biology and management* Alaska Sea Grant Report No. 85-3:357–379.

Lough, R. 1975. Dynamics of crab larvae (Anornura, Brachyura) off the central Oregon coast, 1969-1971. Doctoral dissertation, Oregon State University.

Martin, M., K.E. Osborn, P. Billig & N. Glickstein. 1981. Toxicities of ten metals to *Crassostrea gigas* and *Mytilus edulis* embryos and *Cancer magister* larvae. *Mar. Pollut. Bull.* 12:305–308.

McConnaughey, R., D. Armstrong & B. Hickey. 1995. Dungeness crab (*Cancer magister*) recruitment variability and Ekman transport of larvae. *ICES J. Mar. Sci.* 199:167–174.

McDonald, P.S., G.C. Jensen & D.A. Armstrong. 2001. The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. *J. Exp. Mar. Biol. Ecol.* 258:39–54.

McGaw, I.J. 2008. Gastric processing in the Dungeness crab, *Cancer magister,* during hypoxia. *Comp Biochem Physiol, Part A Mol Integr Physiol* 150:458–463.

McMillan, R.O., D.A. Armstrong & P.A. Dinnel. 1995. Comparison of intertidal habitat use and growth rates of two northern Puget Sound cohorts of 0+ age Dungeness crab, *Cancer magister*. *Estuaries* 18:390.

Methot, R.D. 1989. Management of a cyclic resource: the Dungeness crab fisheries of the Pacific Coast of North America. *Marine invertebrate fisheries: their assessment and management*.

Meyers, T.R., T.C. Schirley, S.M. Schirley, A.K. Sparks & J.F. Morado. 1985. A review of Dungeness crab diseases in the Pacific Northwest and Alaska. In: B.R. Melteff, editor. University of Alaska Sea Grant Report 85-3. Presented at the Proceedings of the symposium on Dungeness crab biology and management. Fairbanks, Alaska, USA: University of Alaska. pp. 209–222.

Miller, J.J., M. Maher, E. Bohaboy, C.S. Friedman & P. McElhany. 2016. Exposure to low pH reduces survival and delays development in early life stages of Dungeness crab (*Cancer magister*). *Mar. Biol.* 163:118.

Morado, J. & A. Sparks. 1988. A review of infectious diseases of the Dungeness crab, *Cancer magister*. *J. Shell. Res.* 7:127.

Mueller, K. & N. Jefferson. 2019. First detection of the invasive European green crab *Carcinus maenas* (Linnaeus, 1758) on Lummi Nation reservation tidelands. *Harvest Management Division Technical Report* Lummi Natural Resources Department, Bellingham, Washington:74.

NMFS. 2001. Marine fisheries stock assessment improvement plan: Report of the National Marine Fisheries Service National Task Force for Improving Fish Stock Assessments. NOAA Technical Memorandum No. NMFS-F/SPO-56, U.S. Dep. Commerce, NOAA, Silver Spring, MD.

Ogburn, M.B. 2019. The effects of sex-biased fisheries on crustacean sex ratios and reproductive output. *Invertebr. Reprod. Dev.* 63:200–207.

Olson, R.E., K.L. Tiekotter & P.W. Reno. 1994. *Nadelspora canceri N. G., N. Sp*., an unusual microsporidian parasite of the Dungeness crab, *Cancer Magister*. *J. Eukaryot. Microbiol.* 41:349–359.

Quentin Grafton, R. 2010. Adaptation to climate change in marine capture fisheries. *Mar. Pol.* 34:606–615.

Rasmuson, L.K. 2013. The biology, ecology and fishery of the Dungeness crab, *Cancer magister*. In: M. Lesser, editor. Advances in marine biology. Vol. 65. Burlington: Academic Press. pp. 95–148.

Reever Morghan, K.J., R.L. Sheley & T.J. Svejcar. 2006. Successful adaptive management: the integration of research and management. *Range. Eco. & Manage.* 59:216–219.

Reilly, P.N. 1983. Dynamics of Dungeness crab, *Cancer magister,* larvae off central and northern California [Marine areas]. *Fish Bull. Cal. Dep. Fish and Game*.

Richerson, K., Punt A. E., Holland, D.S. 2020. Nearly a half centuray of high but sustainable exploitation in the Dungeness crab (*Cancer magister*) fishery. *Fish. Res.* 226.

Sindermann, C.J. 1990. Principle diseases of marine fish and shellfish. In: Diseases of Marine Shellfish. Vol. 2. New York, Boston, London: Academic Press, Inc. pp. 93–144.

Sparks, A.K., J. Hibbits & J.C. Fegley. 1982. Observations on the histopathology of a systemic ciliate (*Paranophrys sp.*) disease in the Dungeness crab, *Cancer magister*. *J. Invert. Path.* 39:219–228.

Sparks, A.K. 1985. Synopsis of invertebrate pathology. Amsterdam, Oxford, New York: Elsevier Science Publishers.

Stevens, B.G., D.A. Armstrong & R. Cusimano. 1982. Feeding habits of the Dungeness crab *Cancer magister* as determined by the index of relative importance. *Mar. Biol.* 72:135–145.

Sulkin, S.D., E. Mojica & G.L. McKeen. 1996. Elevated summer temperature effects on megalopal and early juvenile development in the Dungeness crab, *Cancer magister*. *Can. J. Fish. Aquat. Sci.* 53:2076–2079.

Uhlmann, S.S. & M.K. Broadhurst. 2015. Mitigating unaccounted fishing mortality from gillnets and traps. *Fish Fish.* 16:183–229.

Visser, E.P., P.S. McDonald & D.A. Armstrong. 2004. The impact of yellow shore crabs, *Hemigrapsus oregonensis*, on early benthic phase Dungeness crabs, *Cancer magister*, in intertidal oyster shell mitigation habitat. *Estuaries* 27:699–715.

Walters, C.J. 2007. Is adaptive management helping to solve fisheries problems? *Ambio* 36:304–307.

Whitlow, W.L. 2009. Changes in survivorship, behavior, and morphology in native soft-shell clams induced by invasive green crab predators. *Mar. Eco.* 31(2): 418-430.