SETTLEMENT PREFERENCES OF THE PACIFIC SEA NETTLE, *CHRYSAORA FUSCESCENS*, AND THE SOCIOECONOMIC IMPACTS OF JELLYFISH ON FISHERS IN THE NORTHERN CALIFORNIA CURRENT

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THESIS ABSTRACT

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Title: Settlement Preferences of the Pacific Sea Nettle, *Chrysaora fuscescens*, and the Socioeconomic Impacts of Jellyfish on Fishers in the Northern California Current

Few data are available on distribution, abundance, and ecology of scyphozoans in the Northern California Current (NCC). This thesis is divided into four chapters, each of which contributes to our understanding of a different stage of the scyphozoan life history. The first study describes the settlement preferences of *Chrysaora fuscescens* planulae in the laboratory. Planulae were found to respond to the interaction of substrate and orientation. Artificial substrates were identified as viable habitat for *C. fuscescens*. In the second chapter, a population of scyphistomae in Charleston, Oregon were identified to species-level using DNA barcoding techniques. The third and fourth chapters focus on the medusa stage of the life history. Using surveys mailed to fishers in the Pacific Region, this study provides baseline data on the types and magnitudes of economic damages caused by jellyfish on different fisheries and helps assess fishers' perceptions of jellyfish population trends in the NCC.

This thesis includes previously unpublished co-authored material.

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CHAPTER I

GENERAL INTRODUCTION

Jellyfish Life History

The dimorphic life history of most cnidarian jellyfish is well suited to capitalize on changing environmental conditions. A benthic polyp phase, present in most scyphozoans and hydrozoans, is perennial, and capable of withstanding starvation, salinity fluctuations, and oxygen shifts (Prieto et al., 2010; Purcell et al., 2001). Only millimeters in size, polyps have been shown to possess numerous asexual reproductive strategies (e.g. Condon et al., 2001; Hoffman et al., 1978; Willcox et al., 2007), including budding and the production of podocysts (aggregations of epidermal cells and amoebocytes surrounded by a chitinous cuticle), often produced from the stolon of a polyp, from which additional polyp clones may later develop (Arai, 2009; Dawson and Hamner, 2009). In an asexual reproductive process termed "strobilation," polyps within the class Scyphozoa (scyphistomae) undergo transverse fission, and each segment breaks off the polyp body as a juvenile jellyfish, or "ephyra," which then develops into a mature medusa. One *Aurelia aurita* polyp—a species that has polydisc strobilation—is capable of releasing up to 30 ephyrae per strobilation under laboratory conditions (Lucas, 2001). The polyp stage, therefore, directly influences medusae abundance, and almost all jellyfish species that occur in blooms or aggregations have polyps that undergo strobilation (Dawson and Hamner, 2009). Though larger and more conspicuous, the pelagic medusa phase of the life history is also ephemeral, living only a matter of months. Medusae reproduce sexually by shedding gametes from their oral arms. Fertilization occurs in the water column or within the gonads of the female and the embryos develop

into oblong, ciliated larvae termed planulae. Planulae drift in the plankton for a few hours to up to ten days until they find a suitable hard substrate on which to settle and metamorphose into a polyp (Arai, 1997). This thesis addresses multiple aspects of the jellyfish life history, including the planula, polyp, and medusa stages.

Although the term "jellyfish" technically refers to organisms in the phylum Cnidaria within the class Scyphozoa, in chapters four and five of this text it also will be used to encompass Hydrozoans (Cnidaria: Hydrozoa) and salps (Chordata: Thaliacea). The life history of hydrozoans is similar to that of scyphozoans except that the benthic stage—or "hydroid"—is usually colonial, each colony sharing a gastrovascular cavity (Mills et al., 2007). Salps, in contrast, superficially resemble jellyfish in their gelatinous morphology but are taxonomically quite distinct. Salps are pelagic tunicates—one of the most basal members of the chordate phylum, estimated to have diverged from jellyfish 800 to 900 million years ago (Schopf, 1991). This divergence is evident in their disparate life history: salps, rather than alternating between a benthic and a pelagic stage, are holoplanktonic and alternate between an asexual solitary and a sexual colonial stage, relying primarily on sexual reproduction to increase populations (Boero et al., 2008). Despite great evolutionary distance and ecological dissimilarity (e.g. Condon et al., 2012), salps are included in this analysis because of their propensity to form dense seasonal blooms in the California Current (e.g. Berner, 1967; Lavaniegos and Ohman, 2003; Madin et al., 2006).

Jellyfish Population Trends

Although a "bloom" technically refers to the "normally and abnormally abundant seasonal appearance of jellyfish directly attributable to population growth" (Dawson and

Hamner, 2009), it often describes jellyfish temporarily aggregated by currents or wind (Condon et al., 2012; Graham et al., 2001). The medusae that comprise blooms have large, water-laden bodies with relatively low carbon content; this enables rapid, economical growth when conditions are optimal (Acuña et al., 2012; McHenry and Jed, 2003). These blooms may confer an evolutionary advantage by deterring predation, reducing advection, increasing feeding success, or increasing concentration of gametes and, subsequently, increasing fertilization success (Dawson and Hamner, 2009).

Unsurprisingly, however, blooms have proven problematic for an array of human pursuits: stinging swimmers, clogging power plant intakes and causing shut-downs, killing maricultured fish and bivalves, and interfering with catch fisheries (Purcell et al., 2012). In the past twenty years, prominent and frequent blooms have been documented in oceans worldwide, including South Africa (Lynam et al., 2006), the Gulf of Mexico (Graham 2003), the Mediterranean (Doyle et al., 2008), and the East Asian Marginal Seas (Uye, 2008). This has led to a paradigm in which changing environmental conditions may promote the proliferation of pelagic Cndiarians at the expense of fish. In areas where jellyfish increases have occurred, the primary drivers include climate change, eutrophication, coastal pollution, exotic species introductions, overfishing, and coastal sprawl (Duarte et al., 2012; Lynam et al., 2006; Mills, 2001; Richardson et al., 2009; Purcell et al., 2007).

Many gelatinous species bloom each year as a natural part of their life history, however, and evaluating the concerns about the "rise of jellyfish" is immensely difficult because long-term datasets on jellyfish population cycles are lacking and in many cases nonexistent. Despite worldwide distribution, jellyfish have often been regarded as an

insignificant component of the marine ecosystem. Therefore, it is difficult to ascertain whether jellyfish blooms are increasing relative to historical levels, or rather if blooms are receiving greater recognition because of increased human activity in coastal systems. Condon et al. (2012) recently addressed this question by placing existing data sets on contemporary blooms within their evolutionary context; they concluded that insufficient data existed to form any conclusions on the trend of gelatinous zooplankton populations. In a second, statistical analysis of all available long-term datasets on changes in jellyfish abundance across multiple coastal stations, a weak but significant overall increase in jellyfish since 1970 was identified, as well as a strong recurrent pattern of decadal oscillations that has persisted for over a century (Condon et al., 2013).

Jellyfish and Fisheries

Regardless of the lingering ambiguity about the trend of global jellyfish blooms, it is unquestionable that jellyfish pose a nuisance to fishers around the world in varying degrees. Jellyfish medusae are carnivorous: they consume zooplankton and ichthyoplankton, and therefore can compete with fish species that have similar dietary preferences (e.g. Purcell et al., 2007). Although dietary preferences vary by species, jellyfish generally show preference for fish eggs and larvae, perhaps because these are relatively large plankton with limited to no motility and therefore have higher encounter rates with the jellyfish tentacles (Purcell and Arai, 2001). It is important here, however, to differentiate salps from the umbrella term "jellyfish" because salps occupy a distinct predatory role. Whereas jellyfish medusae are predators that capture prey on their marginal tentacles, salps filter-feed by straining particles through a mucous net (Sutherland et al., 2010). Salps ingest any particles that adhere to the filtering mesh,

including phytoplankton and submicrometer particles such as marine colloids (Dubischar and Bathmann,1997; Sutherland et al., 2010;). Salp grazing, therefore, removes phytoplankton biomass and nutrients from the surface mixed layer. The abundance of Australasian snapper (*Pagrus auratus*) larvae is negatively correlated with the abundance of *Thalia democratica* and *Salpa fusciformis,* suggesting that salp grazing may reduce the survival of some ichthyoplankton (Zeldis et al., 1995). Further study is needed to confirm how salp grazing affects fish, however, since inverse correlations are insufficient to confirm predation effects (Purcell and Arai, 2001).

The relationship between jellyfish and fish is neither limited to trophic interactions nor exclusively competitive. Jellyfish may transmit digenetic trematodes (parasitic flatworms) to fish (Martorelli, 2001); alternatively, fish may commensally remove parasitic hyperiid amphipods from medusae (Riascos et al., 2012). Some fish consume jellyfish—including blue rockfish (*Sebastes mystinus*), one of the more important recreational species for nearshore fishers in the Pacific Region (Coldiron, 2007). The critically endangered Pacific populations of leatherback sea turtles (*Dermochelys coriacea*) seasonally forage on scyphomedusae and siphonophores along the Pacific Coast (Houghton et al., 2006). Some larval and adult fish also consume salps (Fortier, Le Fèvre, and Legendre, 1994). The contribution of coelenterates (Cnidaria and Ctenophores) as prey organisms is likely to be underestimated because gelatinous tissue is digested rapidly, and therefore may not be accurately represented in stomach content analysis of predators (Arai, 2005).

In addition to the indirect impact of reducing recruitment of some fish stocks, medusae blooms can significantly disrupt local fisheries by forcing vessels to relocate, or

by inconveniencing fishers when they retrieve their harvest. Depending on the fishery, the damages can take various other forms, including fouling gear, bursting nets, stinging captured fish and spoiling their commercial value, or increasing the sorting time of bycatch. In Japan, for example, blooms of the moon jelly *Aurelia aurita* have imposed significant costs on the fisheries industry by fouling mackerel purse-seines (Uye and Ueta, 2004) and by consuming almost 100% of mesozooplankton (e.g. copepods and polychaete larvae) that is also preyed upon by commercially-important planktivorous fish (Shoji et al., 2005; Uye et al., 2003). Blooms of another species, *Nemopilema nomurai*, the 200-kg Nomura's jellyfish, clogged and burst the set-nets of fishers along almost the entire Japanese coast in the early 2000s, eliciting complaints from more than 100,000 commercial fishermen (Uye, 2008). The spotted jellyfish *Phyllorhiza punctata* has been estimated to cost millions of dollars to the shrimp industry in the Gulf of Mexico (Richardson et al., 2009). Clearly, competition exists between jellies, finfish, and fishers in many parts of the world.

Jellyfish in the Northern California Current

The Northern California Current is an eastern boundary current that extends from the Strait of Juan de Fuca to Cape Mendocino, California (Barth et al., 2005). It is an upwelling system that experiences high seasonal productivity because of its strong summertime wind-forced upwelling of cold nutrient-rich water. Interannual productivity significantly varies with large-scale climate dynamics such as the Pacific Decadal Oscillation and the El Nino/La Niña Southern Oscillation Cycle (Barth et al., 2005). Local features and conditions, such as banks, eddies, upwelling shadows, and river input, are superimposed upon regional circulation and productivity (e.g. Graham 1993, 1997).

Localized biological hotspots exist throughout the region, structured by regional flow and circulation patterns (Reese and Brodeur, 2006). Blooms of large medusae appear seasonally in the Northern California Current, reaching peak abundance in late summer or early fall (Shenker, 1984). The abundance and distribution of medusae in the Northern California Current varies in response to environmental changes that are controlled by basin-scale climate processes such as horizontal advection (Suchman and Brodeur, 2005). Medusae aggregations may be caused by coordinated swimming behavior, weak surface flow, or synchronous production of ephyrae by the polyps (Suchman and Brodeur, 2005).

Very few data are available on distribution and abundance of jellyfish off the West Coast of the U.S. As noted previously, estimating jellyfish abundance is extremely difficult because of high seasonal and annual variation; jellyfish are also difficult to sample with traditional techniques because nets frequently destroy them. Physical forces such as sea surface-temperature and salinity govern jellyfish abundance in the Northern California Current, but mechanisms responsible for jellyfish population variability are still being uncovered (Suchman et al., 2012). Time-series of observations of pelagic tunicate abundance in the California Current extends for 53 years (Condon et al., 2013). CalCOFI data on jellyfish density in Southern California show significant increases, and anecdotal evidence suggests jellyfish populations along the Central California coast also may be increasing (Brotz, 2011), although an earlier study of pelagic tunicate abundance off the coast of California documented the opposite trend (Lavaniegos and Ohman, 2003).

Older scientific literature provides evidence that mass jellyfish blooms are not a new phenomenon in marine ecosystems. Herrick (1889) elegantly recounts how “we

sailed through a school of medusae which must have covered many square miles of ocean. They were little brown bells, the size of thimbles, and the indigo water was covered with them" (p. 407). Although this particular description is from the Gulf Stream, similar accounts are related in the California Current: Galigher (1925) mentions "hordes of jellyfish which appear annually" (p. 94) along the shores of Monterey Bay, California. Myers and Wales (1930) describe how, in summer, an oceanic current enters Monterey bay at its southernmost point and sweeps the shoreline toward the bay, bringing "great numbers of jellyfish (*Aurelia*)" and attracting small *Mola mola* (p. 11). Salp abundance in the Pacific is also well-documented in historical literature: "they [various species of Salpa] are often so abundant that a bucket of water dipped at random from the surface of some sheltered bay will be found to contain many hundreds or even thousands" (Brooks, 1876, p. 643). William Emerson Ritter—the first director of Scripps Institution of Oceanography—published a report on his work at the San Diego Marine Biological Station during 1908, in which he observes that eight species of salps occur in the area of the Pacific surrounding the biological station. He states, "*Salpa fusiformis-runcinata* clearly heads the list [of abundance], *S. democratica-mucronata* comes next, then, though not quite certainly, *Cyclosalpa affinis*…" (p. 330). He observes that *Salpa fusiformis-runcinata* swarms in early June, while *S. democratica-mucronata* "comes in the millions by July."

A historical perspective of blooms is a useful prerequisite when considering the recent reports of jellyfish abundance in the California Current—most of which focus on the negative social consequences of such abundance. On April 26, 2012, for example, the Diablo Canyon Nuclear Power Plant in San Luis Obispo, California, was forced to shut

down its Unit 2 reactor when southerly winds blew thousands of *Salpa fusiformis* into the reactor's water intake systems (*San Francisco Chronicle Associated Press,* 2012). The sudden, large numbers of salps ripped the trawl nets of NOAA's Southwest Fisheries Science Center while conducting a survey off the central California coast (Esser, 2013). Another salp species (*Thetys vagina*) reached abrupt abundance in Washington's coastal waters in February, where they became ensnared in crab pots (Esser, 2013). In April 2009, a bloom of *Chrysaora fuscescens* in San Francisco Bay stung multiple recreational swimmers (Fimrite, 2009). On July 15, 2012, warm currents from the south carried masses of *Chrysaora achlyos* and *C. colorata* into San Diego Bay, stinging 160 people at seven beaches north of La Jolla (Powell, 2012). Such events, however, should not be equated with a long-term change in jellyfish population trends; increased anthropogenic activity in the marine environment increases the probability of jellyfish encounters. A purported increase in jellyfish interference may simply reflect increased media reporting or heightened public perception of the subject (e.g. Condon et al., 2012; Gershwin et al., 2010; Macrokanis et al., 2004).

Ecologically, jellyfish impact the critical prey resources that support the pelagic fishes of the California Current ecosystem (Brodeur et al., 2008). The four most abundant large medusae in this system are *Chrysaora fuscescens, Aurelia labiata*, *Phacellophora camtschatica*, and *Aequorea* sp[1]. In California, *Chrysaora* (*Pelagia*) *colorata* and *Chrysaora achlyos* can sporadically appear in large numbers in southern California (Martin et al., 1997; Dave Wrobel, Monterey Bay Aquarium, personal communication,

[1] Although it was previously mentioned that "almost all jellyfish species that occur *en masse* strobilate," *Aequorea* sp.—the largest hydromedusa—is a notable exception to this rule (Pitt and Purcell 2008). There is uncertainty about the taxonomic status of *Aequorea.* The scientific literature uses at least three different species names (*Aequorea aequorea*, *A. forskalea*, and *A. victoria*), but these are suspected to all constitute one species (Suchman et al. 2012).

29 September, 2012). Jellyfish are the dominant zooplankton consumers in the system in late summer, consuming almost twice as much zooplankton production as forage fishes (Ruzicka et al., 2007). We have an incomplete understanding, however, of the subtler, indirect ways medusae may influence the food web in the Northern California Current beyond zooplankton consumption.

The primary focus of this thesis is the scyphomedusa *C. fuscescens*, the most abundant semaeostome species in the Northern California Current (Suchman and Brodeur, 2005)—in part because it was the species hypothesized to impose the greatest economic losses to fishers in this region, but also because much work remains to characterize the way in which the seasonal abundance of its medusae is influenced by life history patterns. The remainder of this thesis is divided into four independent chapters, each of which contributes to our understanding of a different stage of the scyphozoan life history. The first study describes the settlement preferences of *C. fuscescens* planulae in laboratory in order to better understand the surface properties influencing settlement and to predict the location of scyphistomae populations in the field. In the second chapter, molecular techniques are used to identify whether a population of scyphistomae in Charleston, Oregon were polyps of *C. fuscescen*s. This chapter was conducted as part of an in-class project in Dr. Svetlana Maslakova's Marine Molecular Biology, BI 457/557, and was written in collaboration with Susan Brush. The third and fourth chapters identify the socioeconomic impacts jellyfish medusae impose on fishers in the Northern California Current.

CHAPTER II

SETTLEMENT PREFERENCES OF *CHRYSAORA FUSCESCENS*

Introduction

Despite the increased recognition that jellyfish blooms have received from scientists and media since the early 2000s, our understanding of scyphozoan population dynamics remains severely hindered by our ignorance of the benthic polyp stage of most species. Although thousands of hours of SCUBA surveys have been devoted to attempting to locate scyphistomae in the field (e.g. Duarte et al., 2012; Heistuman, 1994; Hoover and Purcell, 2008; Toyokawa, 2011a; Willcox et al., 2008), an understanding of the life cycles of most scyphozoans under natural conditions remains incomplete—the polyps proving elusive. Identifying the habitat of the bloom-producing scyphistomae is compounded by their preference for habitat that is difficult to sample; shaded horizontal under-surfaces are the preferred settlement location, perhaps to avoid sedimentation (Arai, 1997). Furthermore, polyps can be cryptic due to their relatively small (< 8 mm) size and potential to be occluded by other benthic organisms.

The lecithotrophic planula represents a critical stage in the jellyfish life history by providing a passageway from the pelagic (medusa) to the benthic zone (scyphistoma). Benthic scyphistomae enable scyphozoans to survive periods of unfavorable environmental conditions, triggering seasonal blooms of new medusae when conditions become more favorable (e.g. Boero et al., 2008). By selecting a particular substrate on which to settle and metamorphose, the planula phase of the life history helps to determine the distribution of adult medusae.

Planulae interact with a surface before settling, and may be highly selective in choosing a substrate (e.g. Arai, 1997). Settlement is a process with two phases: the first, a behavioral searching phase, and the second, a phase of metamorphosis and permanent attachment to the substratum (Rodriguez et al., 1993). In this latter stage, larvae are capable of metamorphosing, but retain their adaptations for existence until a substratum suitable for settlement is found. To prospect habitats, marine larvae possess sensory cells and/or organs, whose capabilities peak at the time of settlement and metamorphosis, and subsequently often degenerate (Crisp, 1974). Marine larval sensory structurs are known to react to light, gravity, pressure, salinity, and water currents, or a hierarchy of multiple sensory cues (Kingsford et al., 2002). Biofilms are complex three-dimensional assemblages of microorganisms (e.g. bacteria, diatoms, fungi, thraustochytrids, and protozoa) that develop on a substrate; the presence of natural microbial biofilms—or even the presence of certain taxa of microorganisms—has been identified as an additional influence in marine larval settlement for some species (e.g. Shimeta et al., 2012). Planulae lack sensory organs, but possess sensory cells and neurones, as well as long cilia at the anterior end of the larval body that may be used to respond to tactile stimuli (Svane and Dolmer 1995). Substrate orientation and fine-scale relief of the substratum surface are among the important determinants of settlement suitability for planulae (Brewer, 1976, 1978, 1984; Cargo, 1979).

The proliferation of artificial structures in the coastal zone is hypothesized to contribute to the increased frequency of jellyfish blooms in some regions by proving unoccupied, protected, floating substrates for the benthic polyps (Duarte et al., 2012). The validity of this hypothesis is therefore based on the ability of the dispersive planula

phase to colonize novel artificial substrates introduced into the coastal zone. This mechanism is difficult to demonstrate at the appropriate scale, but it is supported by several experimental studies and field observations. Three previous laboratory studies have examined the settlement preferences of seven species of scyphozoans, and all found that planulae were readily able to colonize synthetic materials such as plastic, brick, and glass (Duarte et al., 2012; Holst and Jarms, 2007; Hoover and Purcell 2009). Settlement preferences can vary significantly between species, however (Holst and Jarms, 2007), and therefore each additional species whose preferences are tested experimentally provides valuable insights into the little-known behavior and ecology of planulae and scyphistomae.

Chrysaora fuscescens is the most abundant scyphozoan in the Northern California Current (Suchman and Brodeur, 2005), and the species that causes fishers the greatest economic losses caused by jellyfish in this region (Conley, this thesis). In addition, its diet overlaps with whitebait smelt, Pacific herring, northern anchovy, and Pacific sardine, and consequently has the greatest potential for competitive interactions with commercially important pelagic fishes (Brodeur et al., 2008). *Chrysaora fuscescens* may play an important trophic role in euphausiid population dynamics by ingesting euphausid eggs (Suchman et al., 2008). Furthermore, aggregations of *C. fuscescens* are closely associated with the presence of the critically endangered leatherback turtle (*Dermochelys coriacea*), which forage on the scyphozoans, as well as salps and other soft-bodied invertebrates (Benson et al., 2007; Graham et al., 2010). The ocean sunfish, *Mola mola*, also preys on *Chrysaora* (Arai, 2005; Dewar et al., 2010). *C. fuscescens* is a principal host to the parasitic amphipod *Hyperoche medusarum* and a potential disperser of

juvenile graceful rock crabs (*Metacarcinus grancilis*), which attach themselves to the medusae (Larson, 1990).

Despite the high seasonal abundance of *C. fuscescens* medusae, documented to reach 64 mg C/m^3 (Suchman and Brodeur, 2005), there are, to the author's knowledge, no reports of the scyphistoma stage of *C. fuscescens* from the field. A broadcast spawner, both sexes release gametes into the water, and some portion of sperm then fertilize some of the eggs to form zygotes (Widmer, 2008) Although the spawning season of *C. fuscescens* is unknown, the scyphistomae are hypothesized to be located on the hard substrate of protected estuaries and embayments, or on rocky shelf reefs (Suchman and Brodeur, 2005). An entire Master's thesis (Heistuman, 1994) was devoted to attempting to locate *C. fuscescens* polyps in Yaquina Bay using SCUBA, but only *Aurelia labiata* scyphistomae were found. While the ephyrae of *C. fuscescens* have never been reported in the field, the mature medusae are retained nearshore within 200 meters depth. One *C. fuscescens* ephya was collected in a plankton tow on F Dock of the Charleston Marina, Charleston, OR on April 14, 2012 (Brush and Sutherland, unpublished data).

The polyps of *Chrysaora pacifica*, a close congeneric of *C. fuscescens*, were recently discovered on stones and the dead shells of the clam *Meretrix lamarckii* within five-meters depth of the Sagami Bay, Japan (Toyokawa, 2011b). The polyps of *C. pacifica* preferred to settle on the concave surface of bivalve shells, or in hollows of the stones (Toyokawa, 2011b). It is possible that *C. fuscescens* polyps may have similar settlement preferences to *C. pacifica*.

The aim of this present work was to investigate the substrates that induce metamorphosis in *C. fuscescens* planulae in order to better predict planulae, and

subsequently scyphistomae, habitat selection in the field. We used an experimental approach resembling those described by Holst and Jarms (2007) and Hoover and Purcell (2009).

Methods

Medusae and gamete collection

Sexually mature *Chrysaora fuscescens* medusae were collected approximately 14.5 nautical miles northeast of Stonewall Banks, OR (44°32'10.11"N, 124° 5'12.16"W) by the Oregon Coast Aquarium on October 25, 2012. Medusae were held in the Aquarium's 400-gallon holding tank for ten days. On November 5, 2012, four medusae were transported in a five-gallon bucket of unfiltered seawater to the Oregon Institute of Marine Biology in Charleston, OR. Medusae were transferred into a clean bucket and kept overnight in a seatable. Effluent water was sampled daily for presence of planulae.

Substrate selection

The experiment was set up on October 31st to allow for substrates to develop a biofilm. Two categories of substrates were tested: estuarine and offshore (Table 1). Estuarine substrates included concrete, Douglas fir, generic expanded polystyrene foam (GEPS), steel, native oyster shells, *Ostrea lurida*, and cultured Pacific Oyster shells, *Crassostrea gigas*. Scallops shells (multiple species), rock, sand, and mud were tested as offshore substrates. A variety of species of planulae are known to settle on Petri dishes in the laboratory (e.g. Gröndahl, 1989; Svane and Dolmer, 1995) and in the past *C. fuscecens* planulae have been cultured at the Oregon Coast Aquarium using roughened Petri dishes for settlement (E. Daly, Oregon State University, personal communication). Scored Petri dishes were therefore tested as an additional substrate. Each substrate

"category" (estuarine, offshore, or Petri dish) constituted a treatment group.

For ease of cutting, fiberglass-reinforced concrete was used, but the fibrous crosshatching was removed to mimic the surface texture of plain concrete. Douglas fir substrates were treated with a copper naphthenate preservative, and steel substrates were treated with Amazing GOOP Coat-It® Two-Part Epoxy sealer. The Environmental Protection Agency has approved copper napthenate, an oilborne preservative, for wood used in construction of boat piers and other large wooden structures subjected to extended periods of wetting or soaking. It has a General Use preservative classification and an environmental risk assessment indicates copper naphthenate is very stable in water under both aerobic and anaerobic conditions. Steel introduced into marine environments is either treated with epoxy or a cathodic-protection system to resist corrosion. Coatings are the number-one protective device for marine structures and epoxy coatings are used on various tidal and offshore structures such as pilings, pipes, and platforms (e.g. Munger, 1992).

The experiment was designed to test the effect of orientation as well substrate. Each substrate category was tested both floating and submerged, except for the sand and mud substrates, which were always submerged. For the floating treatments, each substrate was affixed to the bottom of an 11.5 x 7.5-cm piece of 1-cm thick polyethylene foam (Figure 1). All substrates were 3.5-cm^2. Douglas fir, concrete, and GEPS substrates were each 0.5-cm thick. Steel substrates were 0.1-mm thick. The shells of *Crassostrea gigas* and *Ostrea lurida* were broken into pieces of 3–4-cm^2. To confirm accuracy of size estimates, the exact area of five sample shell pieces was calculated from their contours using the image analysis software ImageJ. The scallop shells were obtained from the

Oregon Institute of Marine Biology teaching collections and therefore could not be broken, so the sizes were more varied, but presumably did not significantly affect the probability of settlement. Sand and mud were poured into circular caps with a total surface area of 7-cm and 1-cm deep.

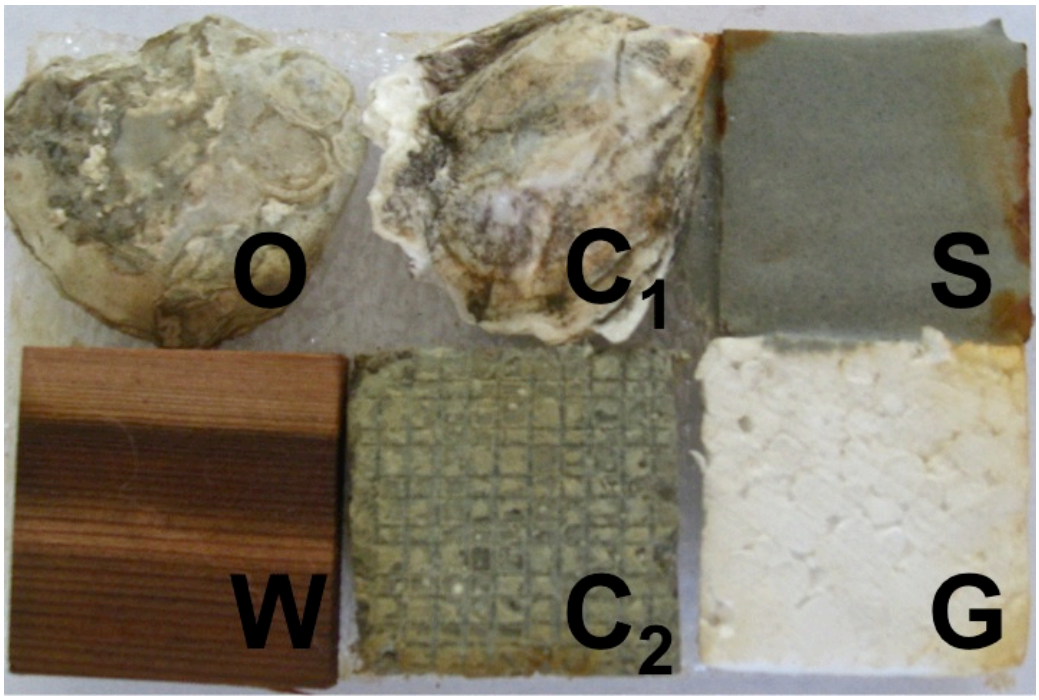

Figure 1. Experimental float with substrates (3.5 cm^2) attached. *O Ostrea lurida*, C_1 *Crassostrea gigas*, *S* steel, *W* wood, C_2 concrete, *G* GEPS.

Thirty-six 0.8-liter plastic containers were arranged in a 6 x 6 array in a seatable. The first row contained submerged estuarine, floating estuarine, submerged Petri dish, floating Petri dish, floating offshore, submerged offshore. This pattern repeated in each subsequent row, but was offset by one to minimize potential error caused by any gradients within the seatable. Each container was filled with 700 mL of seawater filtered through a 10-micron filter bag. In this design, the various substrates in the treatment categories could not be separated and therefore the effects of substrates are somewhat confounded. When planulae settle in the field, however, they are in either a estuarine or

deepwater habitat, so if the two substrate treatment categories were mixed together in the experiment, it would not necessarily be reflective of natural conditions.

The experiment began on November 8, 2012, when the highest abundance of planulae was observed in the effluent water of the mature medusae. Planulae were siphoned from effluent water and filtered into a 250 mL Pyrex® beaker using a 25-μm sieve to create a concentrated solution. Eight milliliters of this concentrated solution (n=177 planulae ± 100) was then pipetted into each replicate container (n=36).

The number of settled planulae on each substrate was first counted on November 17, 2012 using an Olympus SZ61 dissecting microscope. At this stage, many planulae had already metamorphosed and were developing 2-4 tentacles, but a few planulae were still observed swimming. Therefore, an additional count was conducted on November 19—by which time all planulae appeared to have settled. The Nov. 17th counts were compared to the Nov. 19th counts to obtain a rudimentary estimate of the rate of settlement on different substrates, but only the latter data were used for subsequent analysis. Seawater averaged 11.5 ± 1° C during the experiment.

An Anderson-Darling test and a Levene's test of the data showed that both normality and homogenous variance assumptions of ANOVA were violated. Therefore, the data were square-root transformed. This corrected the assumption of homogenous variance (P=0.089), but the data exhibited moderate right-skewness and therefore still deviated from a normal distribution (P=0.006). The ANOVA is quite robust to such minor deviations from the assumption of the underlying population's normality (Zar, 1999) and therefore this deviation was determined not to be substantial. A two-factor factorial analysis of variance (ANOVA) was then conducted on the transformed data

using RStudio to test for effects of substrate type, orientation, and the substrate × orientation interaction on the number of polyps on the substrates, followed by a Tukey HSD Post-hoc test. Because sand and mud substrates were both submerged, and therefore do not accurately test for the effect of orientation, these substrates were excluded from this analysis.

Spatial analysis of settlement

In an attempt to determine whether planulae exhibited gregarious behavior in their settlement patterns, a 6.8 x 4.25-cm sample of polyps settled a Petri dish was photographed using a Sony HDR-CX560V camcorder attached to the dissecting microscope. Photographs were analyzed using the image analysis software ImageJ; settled polyps (n=128) were selected using the multi-point selection tool. The corresponding coordinates were read using R and converted to a point pattern object using the SpatStat package for spatial statistics. Ripley's *K*-function was then used to determine whether the distribution of polyps differed significantly from a Poisson distribution.

Ripley's *K*-function is a tool for analyzing two-dimensional spatial point process data where the theoretical K function is

$$K(t) = \lambda - 1E$$

where *E* is the number of extra events within distance *t* of a randomly chosen event and λ is the intensity (number per unit area) of events (Dixon, 2006; Haase, 1995). It is most often used for spatial pattern analysis in terrestrial plant ecology, but is also a common statistical analysis for samples of benthic invertebrates (Elliot, 1977). It has been applied, for example, to help understand patterns of scallop aggregations (Brand, 2006) and barnacle larval recruitment (Munroe and Noda, 2009).

The *K*-function can be used to assess the fit of point process models, of which homogeneous Poisson process (complete spatial randomness) is the simplest and most often used, where:

$$K(t) = \pi t^2$$

for all *t* (Dixon, 2006). This analysis, however, may underestimate the real number of neighbors within distance *t* because it ignores edge effects, which biases *K(t),* especially with large numbers of points (Goreaud and Pélissier, 1999). Therefore, tests for edge effects are often included in the analysis. Ripley, the edge effect correction used in this analysis, is the most commonly used method of edge effect correction and a review of this and other edge-corrected estimators is available in Dixon (2006).

Results

Larval behavior and development

Mature eggs were approximately 145-µm wide (±13-µm) and 151-µm long (±14-µm). Newly released planulae were yellow, highly motile and approximately 226-µm long (±59-µm) and 97-µm in diameter (±11-µm) (Figure 2a). They were found to be most abundant in the effluent water of medusae that had acclimatized for a few days as opposed to effluent water directly following a disturbance event such as transportation. Planulae appeared within one day of egg release, but a higher abundance of swimming planulae were observed after two days. In one non-experimental beaker, planulae were observed swarming at the water surface. Planulae were determined capable of swimming in still water for up to nine days before settling, and were observed closely exploring potential surfaces before selecting the substrate on which to settle. In this "inspection"

period prior to settlement, planulae reduced their swimming speed, swam millimeters or less above the potential substrate, and, finally, rotated in slow circles the length of their body. As first observed by Widmer (2008b), some planulae settled on the surface tension of the water, but this was much more frequent in non-experimental beakers without floating substrates available. Planulae that settled on the surface tension developed a pedal disk and two rudimentary tentacles, but failed to mature further.

Planulae that settled on experimental substrates developed into polyps by metamorphosing directly after settlement. No encystment of settled planulae was observed on floating substrates, although no attempt was made at differentiating cysts from unhatched eggs on submerged substrates. Yellow pigmentation gradually faded following the development into polyps; four-tentacled polyps had an oral disk width of approximately 0.23-mm and were predominantly translucent with only faint yellow coloration remaining across their oral disk (Figure 2).

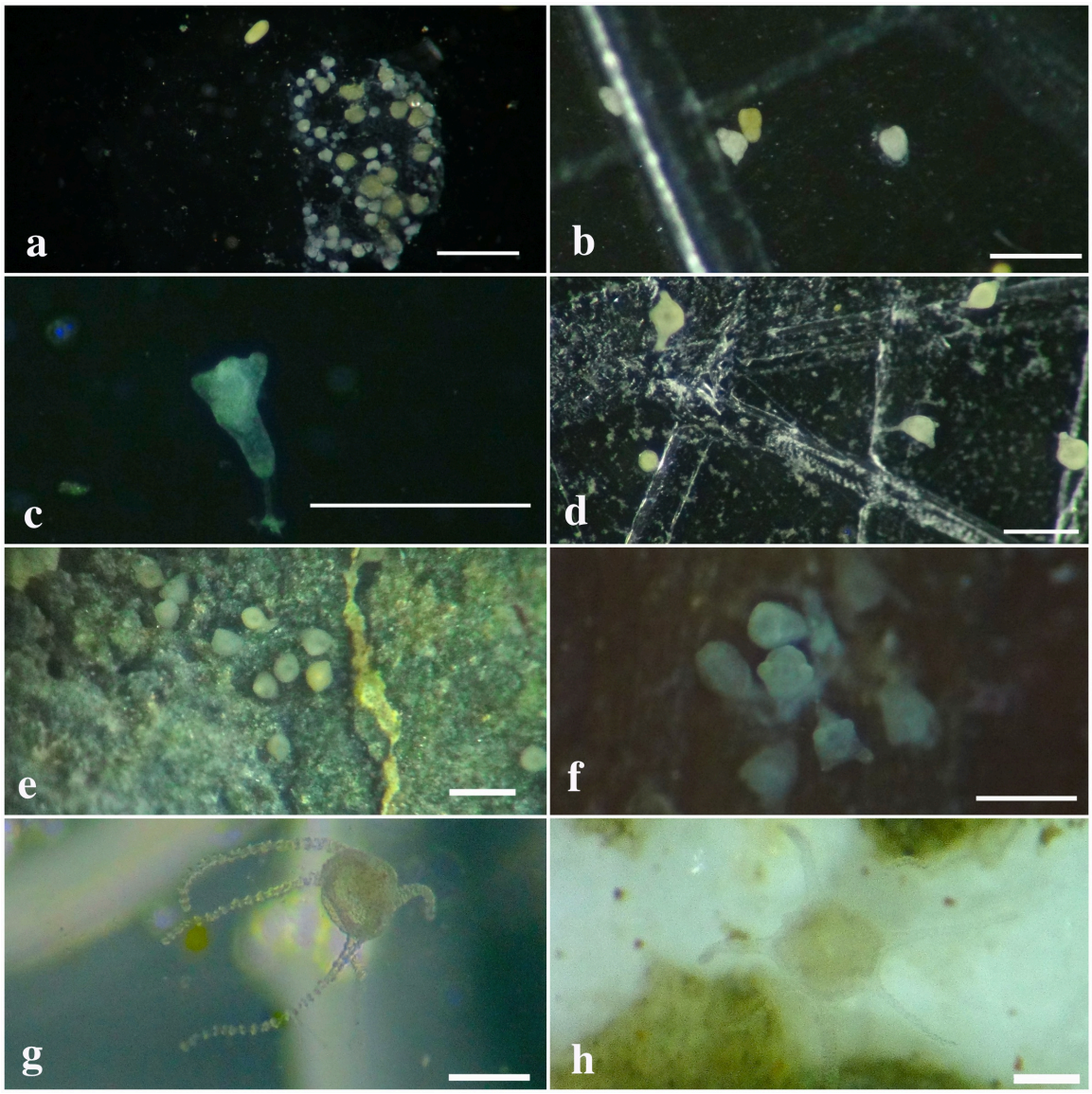

Figure 2. *Chrysaora fuscescens* planulae and metamorphosed polyps in multiple stages of development. **a** close up of a brood pouch from a mature female alongside a single swimming planula **b** planulae attached by their anterior ends to scored Petri dish **c** attachment of planula with two rudimentary tentacles to surface tension of the water by an elongated stalk (pedal stolon) **d** settled scyphistomae with two perradial tentacles **e** newly metamorphosed scyphistomae settled in the pockmarks of rock **f** two- and four-tentacled scyphistomae settled on wood **g** scyphistoma with four filiform tentacles **h** intermediate six-tentacled scyphistoma. Scale bars – 500-µm.

Substrate selection

Figure 3 summarizes the numbers of planulae settled on the nine experimental substrates. Settlement was predictably higher on floating substrates than submerged ones.

The greatest settlement was observed on the floating Petri dishes ($\mu = 156 \pm 47$). Of experimental substrates, settlement was highest on steel. Planulae also showed a strong preference for the undersides of rock, where they tended to cluster in pockmarks. Figure 4 shows the numbers of planulae settled on all experimental substrates to provide an estimate of the rate of settlement on different substrates.

Results from the ANOVA showed significant difference among numbers of settlers on different substrate types ($F_{7, 95} = 4.62$, $P < 0.001$), orientation ($F_{1, 95} = 34.25$, $P < 0.001$), and the interaction between the two ($F_{7, 95} = 4.58$, $P < 0.001$) (Figures 5, 6). A statistically significant preference was identified for steel over all other materials and planulae exhibited a significant aversion to settlement on concrete and bottom sediments. Although preference for rock and wood was not statistically significant compared to that on shells or polystyrene, the mean number of settled polyps on these materials was distinctly higher, suggesting that these substrates are favorable for settlement and metamorphosis of *C. fuscescens*. Again, while not statistically significant, higher settlement was observed on non-native *Crassostra gigas* shells than native *Ostrea lurida* shells.

Spatial analysis of settlement

Spatial pattern analysis using a Ripley's K function gave some evidence for gregarious settlement (Figure 7). The observed value of K(r) for the data pattern of 128 points fell outside of the confidence envelope for the theoretical Poisson distribution pattern—evidence that the null hypothesis of complete spatial randomness may be false. Average intensity was 4.4 polyps per cm^2.

Table 1. Substrates used in testing the settlement preferences of settling planulae of the scyphozoan *Chyrsaora fuscescens*.

Material:	Description:	Groove width:
Steel	Treated with epoxy paint.	< 1 mm
Rock	Granite, granular and phaneritic in texture	< 0.5 mm
Wood	Douglas fir with straight grain, treated with copper naphthenate.	< 1 mm
Crassostrea gigas	Generally deep radial grooves; extremely rough; extensively fluted.	≈ 5 mm ridges/grooves
Ostrea lurida	Radial grooves not apparent; scaly, flaky surface.	≈ 2-3 mm ridges/grooves
GEPS	Rigid white beaded closed cell foam.	0.5-2 mm
Scallop	Broad ribs covered with blunt spines and fine etched striations.	≈ 4 mm
Concrete	Portland cement, the most commonly used cement (Sun et al. 2010); fly ash, expanded clay aggregate, and fiberglass scrim, constituting cement board.	≈ 1 mm
Sand	Very coarse. Components are primarily quartz particles and shell fragments.	Grain size ≈ 1-2 mm
Mud	Silty with an algal film.	Grain size < 62 μm
Petri dish	Scored with knife.	≈ 0.3-0.6 mm

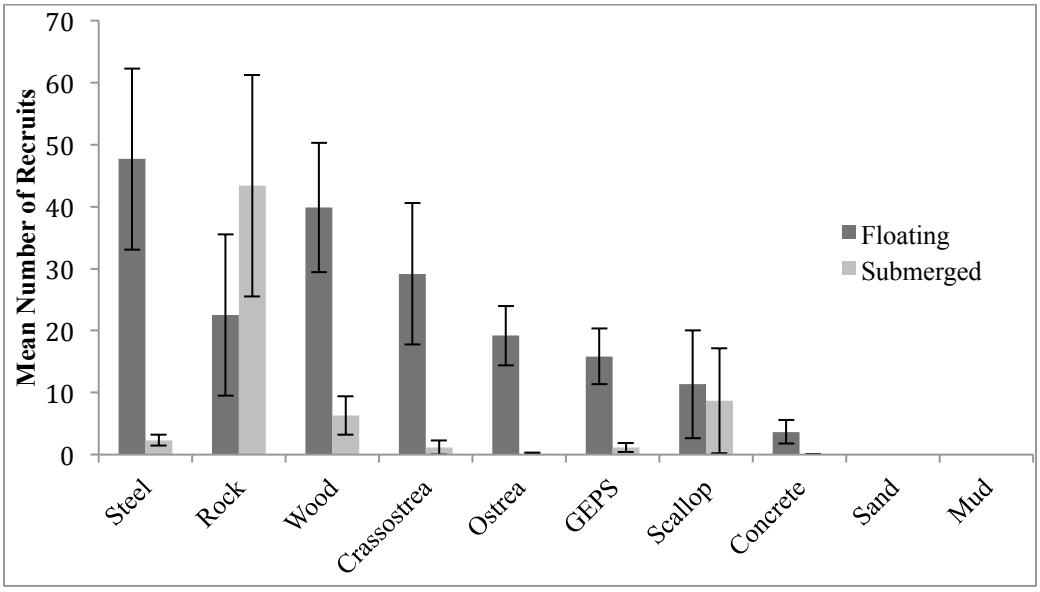

Figure 3. Mean number of settled polyps onto different materials in the laboratory. There were six replicates of each material, except sand and mud (n = 12). Bars indicate standard error.

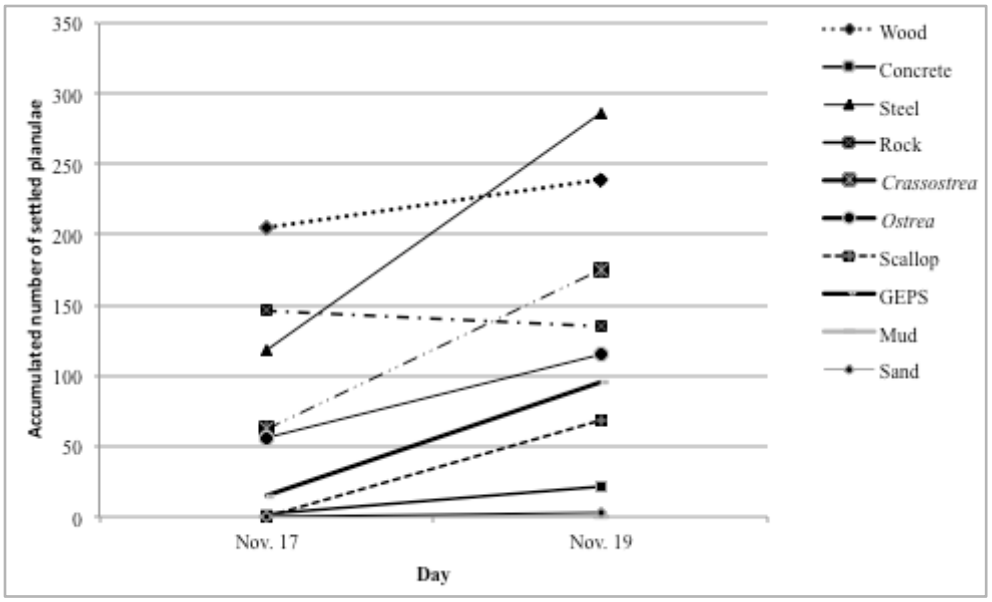

Figure 4. Accumulated numbers of *Chrysaora fuscescens* settlements nine and twelve days, respectively, after the start of the experiment.

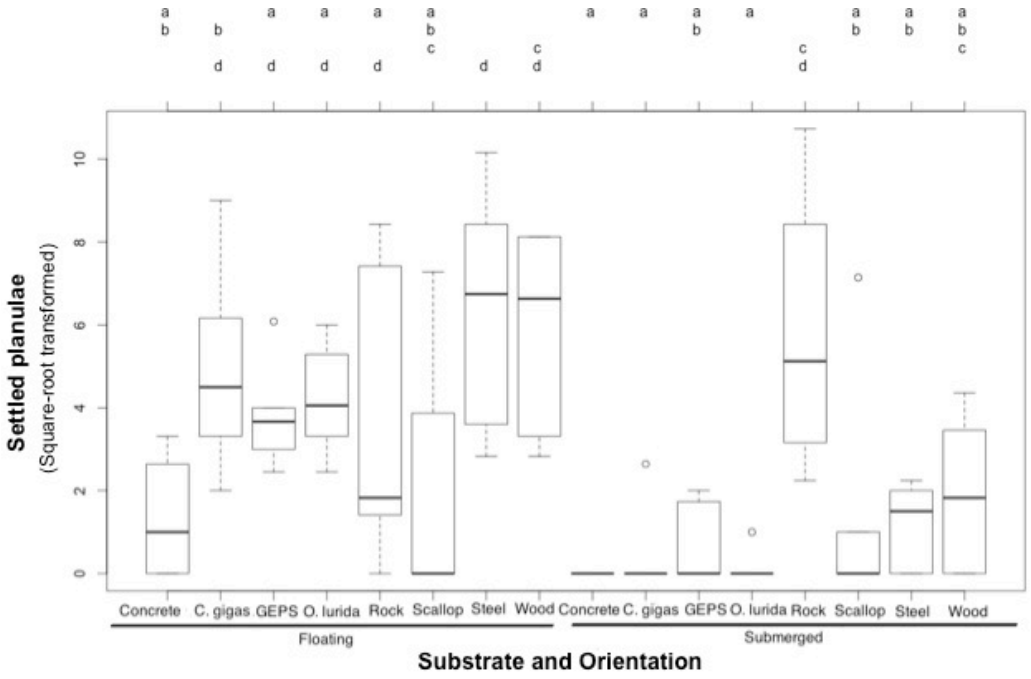

Figure 5. Box-and-whiskers plot developed using R-Studio showing settled *Chrysaora fuscescens* planulae on different experimental substrates and post-hoc labels from Tukey HSD test. The letters A, B, C, and D indicate significantly different groups. Any groups sharing the same letter are not significantly different. In the plots, the box top and box bottom represent the first and third quartile, respectively; the horizontal line in the box shows the median; whiskers show the range; and circles at the top of range indicate only one sample reached this level. Y-axis intervals represent square-root transformed values of settlers obtained from six replicates of each material.

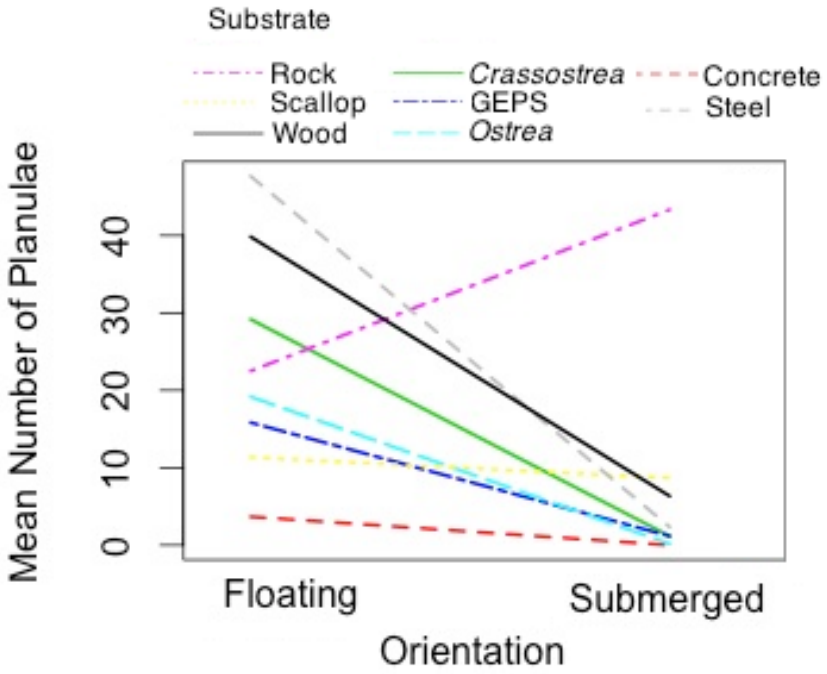

Figure 6. Two-way interaction plot developed using R-Studio showing the mean number of *C. fuscescens* settled planulae for two-way combination of substrate type and orientation. Steeper slopes indicate stronger interaction. Y-axis intervals represent exact (untransformed) values of settlers obtained from six replicates of each material.

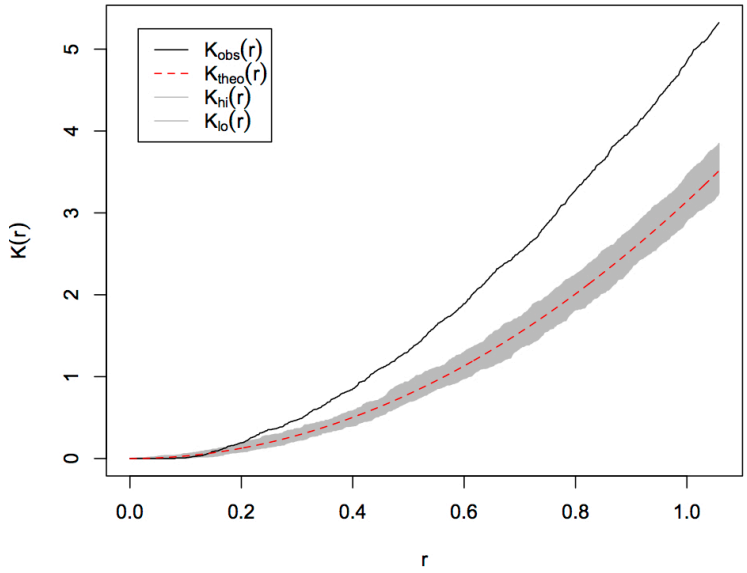

Figure 7. K-function developed in R with the SpatStat package showing the distribution of settled polyps as a function of the scale of measurement (cm, indicated on the x axis). The red K-Poisson line indicates expected K values with K_{hi} and K_{lo} representing the upper and lower pointwise envelope of K(r) from simulations, respectively. Values larger than the K_{hi} envelope (pictured) indicate gregarious behavior, while observed values lower than the K_{lo} suggest overdispersion.

Discussion

In this study, settlement of *Chyrsaora fuscescens* planulae was found to significantly depend on the interaction between substrate and orientation. Artificial substrates (e.g. steel, copper-naphthenate treated wood, and rock) were identified as viable habitat for *C. fuscescens*. Shells received intermediate settlement. Higher settlement on non-native *Crassostra gigas* shells than native *Ostrea lurida* shells may have occurred because *C. gigas* shells are harder, whereas *O. lurida* shells are flaky and may slough off settling organisms over time (Brian Allen, Puget Sound Restoration Fund, personal communication 6 December, 2012).

Marine larval settlement behavior may be influenced by multiple factors, including associative settlement, gregarious settlement, microbial films, hydrodynamic features, neurophysiological cues, and naturally occurring compounds in the substratum (Pawlik, 1992). Settlement preferences of five scyphozoans from the German Bight, North Sea, including the congener *Chrysaora hysoscella,* have been compared (Holst and Jarms, 2007). Differences in settlement on different substrates were attributed to distinct biofilm development on the various surfaces (Holst and Jarms, 2007). It is unlikely that this variable explains the substrate preferences observed in this study. In pre-experiment trials, planulae settlement did not appear to be facilitated by the presence of microbial films. Planulae readily settled on scored Petri dishes that had not been colonized by microorganisms. This suggests other cues are responsible for triggering settlement in *C. fuscescens*.

Chemical cues associated with the substratum may induce settlement if the substances mimic the action of neurotransmitters (Hadfield and Paul, 2001). Two of the

most favored substrates—steel and wood—were treated with chemical preserving agents. Epoxy, which was used to treat the steel, is a relatively stable, nonreactive compound that is unlikely to signal settlement. Copper naphthenate, which was used to treat the wood samples, is a more reactive molecule that may be able to elicit settlement, but this study does not allow any firm conclusions on whether this influenced settlement of planulae. While the influence of signaling molecules cannot be ruled out, the small-scale hydrodynamics associated with the surface properties of the substrate may play a larger influence than chemicals released from the substrate (e.g. Walters, Hadfield, and Carmen, 1997).

Substratum heterogeneity (grooves of different size or scale) and complexity (combinations of scale) may play a role in determining larval settlement preferences (e.g. Lapointe and Bourget, 1999). This criterion appears particularly important for planulae; jellyfish aquarists recommend starting polyp cultures using a scored Petri dish as opposed to a smooth one, since planulae tend to prefer slight surface rugosity (Widmer, 2008a; K. Sutherland, University of Oregon, personal communication; E. Daly, Oregon State University, personal communication). This preference may partly be due to increased wettability of roughened surfaces (Arai, 1997). Since surface roughness influences boundary layer flow, at the small scales affecting larval settlement, local flow patterns around surface roughness features strongly affect viscosity at the boundary layer (Koehl, 2007). In addition, large-scale hydrodynamics is the primary determinant of the number of competent larvae transported to potential settlement sites (e.g. Qian, 1999; Pawlik et al., 1991).

Surface microtexture that is smaller than the larvae, such as the microbubbles that developed on the steel epoxy, may facilitate settlement if larvae can better adhere to the surface imperfections (Howell and Behrends, 2006) (Figure 8). Discontinuities or microsites within the substrate, such as the pockmarks in the rock and the crevices of the Douglas fir grain, may be preferred because they offer protection from high shear stress (Wethey, 1986). This study found a statistically significant preference for rock over concrete, which is somewhat unexpected since both materials are hard aggregates. At the micro-level, however, the two surfaces have considerably different textures. Basalt is a fine-grained igneous rock (Ibrahim et al., 2009), whereas Portland cement has a larger grain size diameter with millimeter-sized crosshatching, constituting multi-scale roughness components. Barnacle cyprids have been found to respond to scales of surface texture, preferring fine and medium surface roughness to coarse, multi-scale roughness; this preference is hypothesized to maximize adhesion (Hills and Thomason, 2009). Therefore, while this study did not test the effect of flow, perhaps planulae are adapted to settle in locations that diminish hydrodynamic stress, thereby reducing the likelihood of the larva being dislodged.

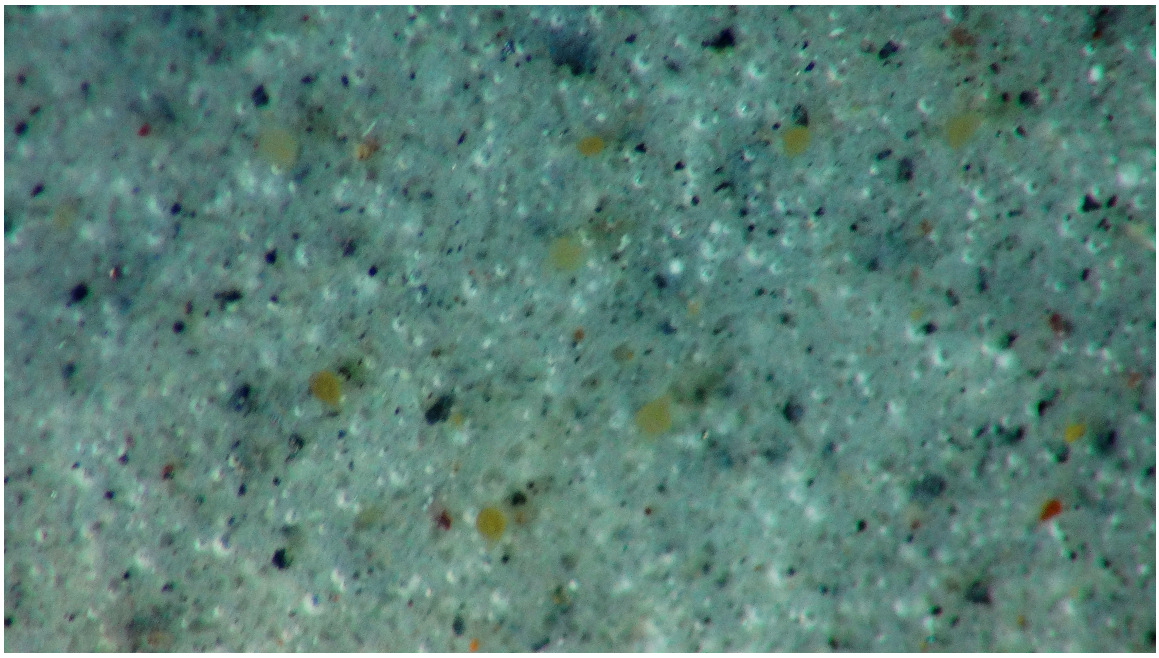

Figure 8. Newly metamorphosed *Chrysaora fuscescens* scyphistomae settled on epoxy-coated steel. Microbubbles add microscopic surface roughness.

Planulae of different species, however, appear to exhibit different preferences for substratum heterogeneity. Wood was among the least preferred substrates of *Aurelia labiata* planulae (measured by mean numbers of planulae settling onto dock-building materials in the laboratory), and instead planulae preferred polystyrene foams, including GEPS (Hoover and Purcell, 2009). All scyphozoans examined by Holst and Jarms (2007) exhibited a preference for polyethylene and a weak inclination for settlement on wood. *Chrysaora fuscescens* therefore exhibit considerably different settlement preferences than previously studied species, since its planulae have a relatively low affinity for settling on plastics and a high affinity for wood. The species-specific nature of settlement response has been identified for other benthic marine invertebrates (e.g. Pawlik 1988) and the observed differences in the settlement preferences of *C. fuscescens* may be attributable to their different preferred habitat in the field. *Aurelia labiata* polyps, for example, are most commonly found on floating anthropogenic structures in estuarine locations, but *C.*

fuscescens may settle on different materials or in a different habitat. Additionally, some larvae preferentially attach in grooves or pockets with widths of similar dimension to the body size of the larva, which may help explain the differences in settlement preferences between species (e.g. Hoipkemeier-Wilson et al., 2004). The diameter of a *C. fuscescens* planula is approximately 85-100-µm (Widmer, 2008b). Comparatively, the larvae of *Aurelia aurita* are considerably smaller, ranging from 34.6-µm to 40.4-µm, depending on the food availability for the adult medusae (Lucas, 2001). Therefore, the association between larval length and settlement preference may help explain the observed differences in settlement patterns between the two species.

One aspect that *C. fuscescens* shares with other scyphozoan species whose settling behaviors have been examined in the laboratory is a strong preference for the underside of substrates (Brewer 1976, 1978, 1984; Cargo, 1979; Pitt, 2000; Svane and Dolmer, 1995). *Chrysaora* planulae had higher settlement on the undersides of submerged rocks than on floating rocks; since the only difference between the floating and submerged rocks is light attenuation, this suggests *C. fuscescens* planulae may be negatively phototactic—a behavioral response that has been observed for other scyphozoan species (e.g. Duarte et al., 2012).

Consistent with existing literature, *C. fuscescens* planulae did not settle on bottom sediments. In the field, because mud and sand are mobile, planulae that settled and metamorphosed on these substrates would be damaged by the bioturbation and tend not to survive (Holst and Jarms, 2007). Even in the laboratory, in the absence of realistic flow conditions, planulae were able to identify these substrates as unsuitable. This suggests that selective pressure has influenced planulae settlement behavior, and that the preferred

substrates are those on which polyps would be most likely to survive in the harsh marine environment (e.g. Brewer, 1984). In some benthic habitats, the sand and mud grains may be too small to settle on; in this study the sand grains were larger than the planulae themselves, but the mud grains, on which no larvae settled, were smaller than the body of the planulae.

Many experiments on the settlement responses of marine invertebrate larvae are designed, as this one, with multiple larvae occupying one experimental container with different substrates available for settlement (Gotelli, 1990). If the larvae being tested exhibit gregarious behavior, the settlement responses are confounded by the distribution of previously settled individuals, creating a problem of non-independence (Gotelli, 1990). This consideration is, of course, not relevant in the absence of gregarious behavior. Additionally, if the goal of the study is, as this one was, to "qualitatively assess which surfaces larvae prefer, gregariousness will not greatly bias the results" (p. 107).

I did not risk examining the settlement preferences of solitary planulae because they exhibit high mortality. I therefore attempted to determine the randomness of larval settlement distribution by comparing settled polyps to an expected Poisson distribution using Ripley's *K*-function. The spatial pattern analysis used a sample of settled polyps (n=128) from one substrate as an indirect indicator of gregariousness of planulae; this method offers some evidence to suggest planulae may be gregarious. No asexual budding was observed in the settled polyps, but if any budding had occurred this would contribute to spatial pattern appearing gregarious. Planulae of *Cyanea capillata* have shown gregarious behavior (Dolmer and Suane, 1993), but different experiments with *Aurelia aurita* planulae have claimed gregarious settlement (Gröndahl, 1989) and that settlement

that is independent of con-specific density (Keen, 1987). Just as different species of planulae have demonstrated different substrate preferences, it is possible that different species possess varying levels of gregariousness. Future studies should focus specifically on evaluating the gregariousness of scyphozoan planulae, since ambiguity is pervasive in existing literature (e.g. Dolmer and Suane, 1993; Gröndahl, 1989; Keen, 1987), and this behavioral characteristic affects experimental settlement responses.

The results had a relatively large standard error, which may be attributable to shortcomings in experimental design rather than variance in larval preferences. The submerged rock samples were placed flat against the bottom of the container; planulae, however, were still able to navigate to the rock underhangs—achieving an inverted orientation akin to that on a floating surface with less light exposure. Planulae settlement may be higher on substrates that planulae can crawl underneath compared to substrates that are raised or floating (Pitt 2000). Observed variance in the experiment may also be attributable to natural variance: the high standard error in settlement on *Crassostrea gigas*, for example, may be explained by the differences in flutings and surface roughness between shell samples.

Larval behavioral responses produce ecological effects by influencing the distribution of scyphistomae. The results of this study are useful in order to predict the source locations of polyps in the field—estuarine locations, rocky shelf reefs, or offshore benthos. In bays off the Oregon coast, juvenile medusae of *C. fuscescens* are found in spring, after upwelling occurs (E. Daly, Oregon State University, personal communication). Mature medusae are retained in nearshore waters (<200-m depth) and are abundant from June to September (Suchman and Brodeur, 2005). The spawning

period of *C. fuscescens* is currently unknown. If medusae spawn in the fall, after downwelling occurs, then the planulae would be more likely to settle on shallow reefs. Alternatively, medusae may spawn during the upwelling season with offshore transport of coastal waters and planulae (Landry and Hickey, 1989). If the latter were the case, polyps would likely be located in offshore waters (E. Daly, Oregon State University, personal communication). Unfortunately, all of these possible locations are difficult to survey, and until *C. fuscescens* scyphistomae are located in the field, we must rely on observations of planulae behavior and polyp development in the laboratory.

Ocean energy is likely to develop in the Pacific Northwest in upcoming years (e.g. Boehlert et al., 2008) and Oregon is already well underway in its initiation of wave energy. Ten PB150 PowerBuoy wave-energy devices are scheduled to be deployed 2.5 miles off the coast of Reedsport, Oregon, each measuring 150 high by 40 feet wide (Loew, 2010). Ocean Power Technologies is proposing to develop a second commercial wave park 2.7 miles west of Coos Bay, Oregon. According to Ocean Power Technologies, the project is expected to be the largest wave-energy project in the world, consisting of up to 200 PowerBuoys and 20 undersea substations. Although no offshore wind turbines have been installed in the U.S., a Stanford University study found that significant development potential exists for offshore wind energy in California, identifying a site off Cape Mendocino as a promising potential farm locale (Dvorak et al., 2009).

These are just a few examples of the many proposed offshore energy projects, which may soon collectively introduce a large volume of steel and concrete substrate for benthic organisms to colonize. Given the observed preference of *Chrysaora fuscescens*

for steel, such development has the potential to provide favorable habitat for scyphistomae, which may in turn alter medusae abundance. Our results indicate that other forms of coastal development may also provide habitat for *C. fuscescens* scyphistomae if oceanographic factors transport planulae to these artificial structures.

Rock and wood, the second and third most preferred substrates, respectively, are natural substrates but are frequently used in coastal development. Wood pilings, for example, are often used in the construction of docks, where *Aurelia aurita* polyps have been observed to settle (Duarte et al., 2012). Shoreline stabilization structures, including breakwaters, riprap, seawalls, groins, and slope revetments, can be made of wood, rock, or a combination of the two. Rock is also a natural substrate both inshore and offshore. In offshore habitats, in particular, rock may be among the few hard substrates available for planulae settlement.

The present study therefore corroborates past studies that indicate the important role of artificial substrates in planulae settlement (e.g. Duarte et al., 2012; Holst and Jarms, 2007; Hoover and Purcell, 2008; Lo et al., 2008), particularly in locations where natural hard substrate is sparse. This research contributes to the growing body of knowledge about the impacts that coastal infrastructure may impose on marine community structure and how such infrastructure may be designed to reduce this impact. Knowledge of the preferred microtexture scales of diatom species, for example, is being used to develop structured surfaces to control the attachment and development of diatom fouling communities (Scardino et al., 2006). Continued examination of the settlement preferences of *C. fuscescens* planulae has similar extrapolative value, both for predicting habitat preference and, with further research, modeling medusae population dynamics in

response to different forms of coastal sprawl. *Chrysaora fuscescens* medusae are of particular ecological importance (Brodeur et al., 2008) and economic consequence (Conley, this thesis), and understanding of the larval and benthic stages is a prerequisite to interpreting population blooms.

CHAPTER III

GENETIC IDENTIFICATION OF SCYPHISTOMAE FROM THE CENTRAL OREGON COAST

This section was written in collaboration with Susan Brush, a fellow member of the Sutherland Lab. I am the sole author of the introduction and discussion sections and the methods and results sections are co-authored. I would like to acknowledge Dr. Maslakova for constructively reviewing this portion of the manuscript, as well as Terra Hiebert for her help with molecular laboratory techniques.

Introduction

Although increased recognition of jellyfish blooms have prompted increased research into the ecology of gelatinous macrozooplankton, most of this research has been devoted to the pelagic phase of the life cycle (medusae). Furthermore, though some planktonic salps (e.g. *Thalia democratica*), siphonophores (e.g. *Nanomia cara*) and leptomedusae (e.g. *Aequorea* sp.) can form massive seasonal surface aggregations, blooms of scyphozomedusae typically reach higher abundances and represent a greater proportion of carbon biomass off the Oregon coast (Mills, 2001; Suchman and Brodeur, 2005).

Unlike other Medusozoans—a monophyletic clade that includes Cubozoa, Hydrozoa, and Scyphozoa (Dawson, 2004)—the life history of scyphozoans is dominated by a large medusoid stage, but most also include a benthic polyp stage (Arai, 1997). The polyp stage remains unknown for many scyphozoans, and little is known about the ecology of the polyps that have been found (Arai, 1997). The species descriptions and

identification keys for scyphozoans are typically based on the medusoid stage and the polyp stage remains in the shade—both figuratively and literally. Most of what is known about the benthic polyp phase of the life cycle, or scyphistomae, is derived from laboratory studies, and little data exists on colonies in the field. It is important to rectify this limited knowledge of scyphistomae ecology because the perennial polyps are presumed to be important drivers of medusae population dynamics (Duarte et al., 2012; Purcell, 2007).

Scyphistomae preferentially settle on the undersides of shaded horizontal surfaces, such as floating piers and wharves (Duarte et al., 2012). In order for colonies to form, a planula larva, produced sexually by the medusae, must first settle on hard substrate and metamorphose into a polyp. Colonies may then grow through three principle mechanisms: continued settlement of additional planulae; asexual budding from mature polyps, producing individual clone genets; or through the production of podocysts from the pedal disk of a polyp (Arai, 2009). These strategies allow scyphistomae to either expand into new, unoccupied substrate, or to increase the density within the existing colony. Scyphistomae typically strobilate as water temperatures increase in spring (Wilcox, 2008), producing ephyrae that develop into mature medusae.

In the field, scyphistoma colonies form dense (150,000-400,000 individuals/m^2) mats that can cover several hundred meters if suitable habitat is available (Hoover and Purcell, 2009; Willcox et al., 2008). Of the published reports of schyphistomae colonies across the world, 70% have been identified as *Aurelia* sp. (Duarte et al., 2012).

At the Charleston Marina Complex on the northwestern shore of Charleston, Oregon, scyphisomae are one of the more abundant fouling organisms on the undersides

of many of the floating dock slips. Because scyphistomae exhibit a great deal of macro-morphological plasticity, traditional morphological identification is challenging. Even invertebrate taxonomic experts have failed to successfully identify scyphistomae to genus level: the North Pacific International Commission for the Exploration of the Seas (PICES) conducted a survey of Oregon's Yaquina Bay, Umpqua Triangle, and Coos Bay to identify fouling invertebrates in an attempt to establish the prevalence of introduced species in Oregon's near shore ecosystems. Despite the observed abundance of Cnidarians on intertidal and subtidal substrata, and the phylum's infamous potential as a catastrophic invasive (e.g. Graham et al., 2007), the PICES rapid species assessment surveys ignored Cnidarians entirely because of the inability to confidently identify individuals to species or even genus level (J. Chapman, Oregon State University, personal communication 7 July, 2012).

Scyphistomae may be identified to species level by collecting individual polyps from the field, resettling them, inducing strobilation, and rearing the released ephyrae to mature medusae. Strobilation is difficult enough to induce in species whose environmental trigger cues are known, and even more difficult and less reliable for species whose cues are unknown. Regardless, the process requires many months—with an undependable outcome (Widmer, 2005). An alternative approach relies on PCR-based methods for the detection and identification of scyphistomae (Bayha and Graham, 2009). We, therefore, attempted to use molecular techniques to identify the scyphistomae in the Charleston Marina Complex.

The phylogeny of many—if not most—scyphozoans lacks resolution, requiring further investigation (e.g. Dawson and Martin, 2001). Cryptic species within the genus

Aurelia have recently been identified, distinguishing *Aurelia labiata* as a distinct species endemic to the North Pacific (Gershwin, 2001). The taxonomic status of *Chrysaora* is also suspect because many species were originally described on the basis of only a few specimens (Larson, 1990).

Forty-three species of scyphomedusae are known in the Eastern Pacific from Alaska to Chile, but only four of these are reported from Oregon (Larson, 1990; Mills and Larson, 2007). Anecdotal reports suggest two additional species may perhaps infrequently drift into Oregon, although no published data exists to confirm this: *Chrysaora melanser* might perhaps stray south from the Bering Sea, and *Chrysaora colorata* (formerly *Pelagia colorata*) may occasionally range north of San Francisco (Mills and Larson, 2007). Therefore, it is possible that the scyphistomae are any of the four resident species*: Chrysaora fuscescens*, *Aurelia labiata*, *Cyanea capillata*, and *Phacellophora camtschatica*. In addition to being the most abundant semaeostomeae in the northeast Pacific, the range of *C. fuscescens* is nearer to shore—primarily within 200-m depth on the continental shelf (Suchman and Brodeur, 2005). The other common species—*A. labiata* and *Phacellophora camtschatica*—are more abundant in deeper oceanic waters. Since *Cyanea capillata* is much less numerous off Oregon than are any of the other three species (Shenker, 1984), it was unlikely that the scyphistomae were *Cyanea.*

Scyphistomae colonies can actively grow for many years without producing ephyrae (Boero et al. 2008). No one to date has reported observing the Charleston Marina scyphistomae strobilate and ephyrae are extremely rare in year-round plankton tows routinely conducted in the Charleston Marina by faculty and students at the Oregon

Institute of Marine Biology. One *C. fuscescens* ephyra, however, was collected in a plankton tow in the Charleston Marina on April 14, 2012 (Brush and Sutherland, unpublished data). Although bi-weekly plankton tows were carried out at that same sampling station until May 31, 2012, no other species of ephyrae were found (Brush and Sutherland, unpublished data). If ephyrae are found entrapped in harbors, one may assume the scyphistomae are nearby (Toyokawa et al., 2011b). Hence, we hypothesized that the scyphistomae in the Charleston Marina are *Chrysaora fuscescens*. We used distance-based DNA barcoding of the mitochondrial locus cytochrome c oxidase I (COI) to assess whether scyphistomae could be identified to species-level using these techniques.

Methods

Morphological characteristics

Although scyphistomae exhibit high morphological plasticity in response to environmental conditions, we compiled morphological data on scyphistomae from the most common scyphozoans in Oregon for comparison with the Charleston marina specimens (Table 2). The Charleston scyphistomae specimens were photographed underwater while snorkeling using a digital camera (Nikon Coolpix AW100) mounted on a 10 x 6-cm quadrat. A Light&Motion SOLAPhoto1200 Focus compact imagine light was mounted to the framing arm and used with High Beam 1200 Lumens white lighting to supplement the camera flash. Scyphistomae morphology was analyzed in the photographs using the image analysis software ImageJ.

Table 2. Morphological character variation of scyphistomae species endemic to the Oregon Coast.

Species	Morphological characteristics of polyps				
	Number of tentacles:	Mean tentacle length (mm):	Mean height (mm):	Mean oral disk width (mm):	Reference:
Aurelia labiata	16-24	Unknown	2-3	1-2	Gershwin 2001
Chrysaora fuscescens	16	1.51	0.88	0.72	Widmer 2008
Phacellophora camtschatica	30–44	17.8	7.95	2.65	Widmer 2006
Charleston scyphistomae	26	4.25	3.3	1.84	This study

Tissue collection and DNA extraction

Tissue was collected from three specimens as described below. A single planula larva was collected from spawning known adult *Chrysaora fuscescens* on October 10, 2012. The larva was preserved at -20° C in a small volume of seawater. DNA was extracted from larval tissue using Instagene matrix (Biorad) on October 15, 2012. Extracted DNA was subsequently stored in -20° C.

A sample of marginal tentacle tissue was collected from *C. fuscescens* medusa on October 5, 2012. Tentacle tissue was preserved at -20° C in a small volume of seawater. DNA was extracted from the tentacle on October 17, 2012 using a column-based extraction method with DNEasy Blood and Tissue Kit (Qiagen). DNA from medusa tentacle was sufficiently amplified (Figure 10).

Scyphistomae were collected on October 17, 2012 and November 6, 2012 from the underside of the floating docks in two different locations in the Charleston Marina Complex (Figure 9). We extracted DNA on October 17, 2012 using the DNEasy Blood

and Tissue Kit (Qiagen). Scyphistomae DNA was amplified on October 31, 2012 and did not produce DNA of sufficient quantity or quality (Figure 10).

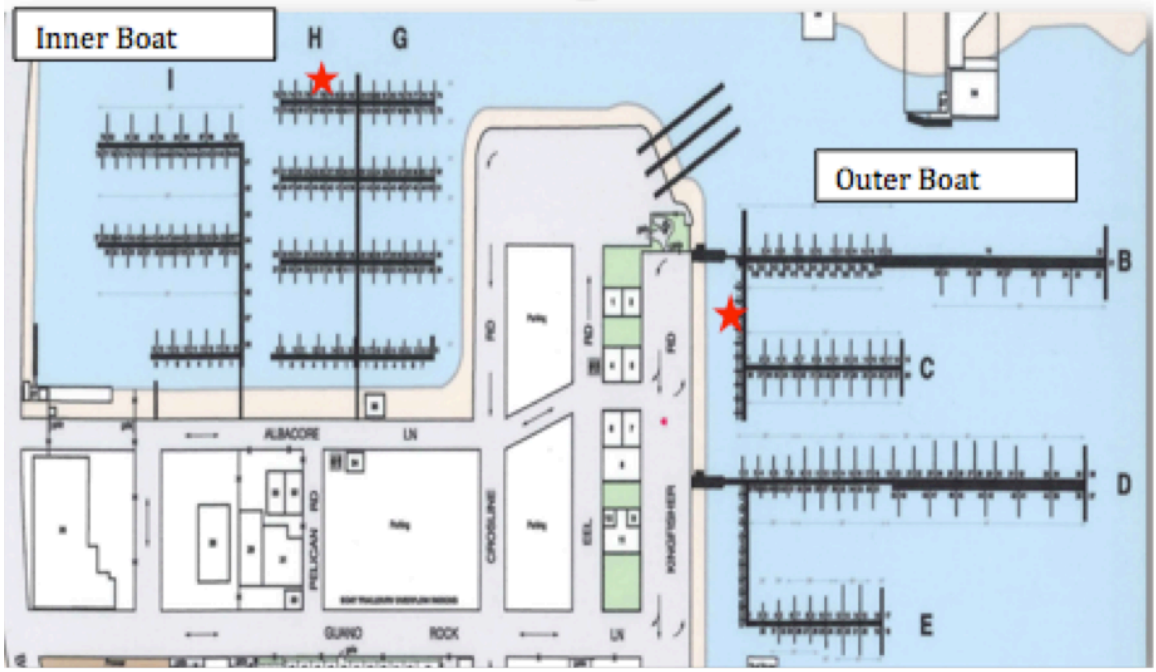

Figure 9. Map of scyphistomae sampling sites Charleston Marina, Charleston, OR. Sampling sites indicated by red stars.

According to methods by Pinto et al. (2000), tissue was lysed by grinding samples thoroughly using a sterile single-use pestle with 180-ul of ATL Buffer and 20-ul of Proteinase K (Qiagen, DNEasy Blood and Tissue Kit) and incubated overnight at 37° C in a thermomixer. We extracted DNA using the following modified phenol-chloroform protocol: equal volume of buffer saturated phenol-chloroform-isoamyl alcohol (#9730, Ambion, pH 7.9) was added to each of the three scyphistomae tissue samples and one control sample (nemertean tissue); samples were vortexed for 20 seconds and centrifuged at room temperature for five minutes at 14,000 x g. Upper aqueous phase was transferred to a new tube and procedure was repeated for all samples. After the addition of Glycoblue (AM9516, Ambion), 7.5 M NH4OAc, and 100% EtOH (Table 3), the samples were

placed in -80° C for one hour to precipitate the DNA. Samples were then centrifuged at 4°C for 30 minutes at 14,000 x g. Dark blue pellets were visible in all samples except for one of the scyphistomae samples (sample C2). Supernatant was removed from all samples without disturbing the DNA pellet. The DNA pellet was rinsed in 0.5-ml of 70% EtOH, then briefly centrifuged for 2 minutes at 14,000 x g. Remaining EtOH was removed and pellets were air-dried for 30 minutes, then placed on a 37° C heating block for an additional 45 minutes. DNA was re-suspended in 200-ul of Elution Buffer (DNEasy Blood and Tissue Kit, Qiagen). Presence of Genomic DNA was confirmed on 1% agarose gels (Figure 11).

Table 3. Volumes of precipitation reagents used in phenol-chloroform based extraction of scyphistomae DNA.

Sample	Sample volume	Glycoblue (750 ug/ml)	NH4OAc	EtOH
C1	90 ul	5ul	10ul	300ul
C2	50 ul	2.5ul	5ul	150ul
C3	90ul	5ul	10ul	300ul
Nem.	50ul	2.5ul	5ul	150ul

PCR amplification, purification and quantification

We attempted to PCR-amplify the protein coding gene Cytochrome Oxidase subunit 1 (CO1) using universal and scyphozoan-specific primers (Table 4). Amplifications were performed in a MJ Research PTC-100 Programmable Thermal Controller with the following reagent concentrations: 1x green GoTaq® reaction buffer, 200-uM dNTP mix, 1 unit Go Taq Polymerase and 500-nM primers. The initial denaturation was performed at 95°C for 2 minutes, then 35 cycles of the following: cycle denaturation at 95°C for 40 seconds, primer annealing at 46°C for 40 seconds, primer extension at 72°C for 1 minute on the final cycle, and a final extension at 72°C for 2

minutes.

The size of the PCR products was verified on 1% agarose gels with 0.1 ug/ml of EtBr in 0.5X TBE buffer using 1KB DNA ladder (Promega) (Figure 12). PCR products that appeared as single bright bands of expected size were purified using SV Wizard Gel and PCR clean up Kit (Promega) and quantified on 1% agarose gel with Low Mass DNA Ladder (New England Biolabs) (Figure 13). Sequetech, Inc. (Mountain View, CA, USA) preformed DNA sequencing.

Table 4. PCR primers employed in this study.

Primer name	**Sequence (5' –3')**	**Reference**
LCO1490 (universal)	GGT CAA CAA ATC ATA AAG ATA TTG G	Folmer et al., 1994
HCO2198 (universal)	TAA ACT TCA GGG TGA CCA AAA AAT CA	Folmer et al., 1994
MedCOIR (scyphozoan-specific)	GGA ACT GCT ATA ATC ATA GTT GC	Ortman, 2010
HCO-2607 (scyphozoan-specific)	ACA TAG TGG AAA TGT GCT ACA ACA TA	Ortman, 2010
LCOjf (scyphozoan-specific)	GGT CAA CAA ATC ATA AAG ATA TTG GAAC	Dawson, 2005
HCOcato (scyphozoan-specific)	CCT CCA GCA GGA TCA AAG AAA G	Dawson, 2005

Sequence analysis

Sequences were trimmed and proofread using CodonCode Aligner v. 4.0.4 (CodonCode Corporation) and compared to the GenBank nucleotide database using the NCBI BLAST program (Table 5). Sequences were aligned with additional scyphozoan sequences downloaded from GenBank (Table 6) using ClustalX v.2.0 (SFI) (Larkin et al., 2007). Two phylogenetic trees were assembled: a maximum parsimony tree prepared in PAUP v. 4.0 (Sinauer Associates, Inc.) and a distance tree prepared in ClustalX v.2.0 and viewed in FigTree v.1.3.1.

Results

Three scyphistomae samples and one tentacle sample were sequenced using the COI gene. Scyphozoan-specific and universal primers were used to amplify this region. Sequences obtained from the scyphistomae were identified as *Aurelia labiata* (Table 5). The universal primers amplified contaminant DNA in the scyphistomae samples, identifying sequences as *Eupolymnia heterobranchia* and *Balanus glandula.* The known *Chrysaora fusescens* tentacle sample did not find a close sequence match in the NCBI database.

The Charleston Marina scyphistomae sequences aligned unambiguously with a GenBank sequence of *A. labiata* scyphistomae from Tomales Bay, California (Dawson, 2005) (Figure 14). The Genbank sequence of *A. labiata* scyphistomae collected in Newport, OR (Dawson 2005) had a percentage of sequence distance (P-distance) of 0.15% from the Charleston Marina scyphistomae—a difference of a single base pair.

In the parsimonious tree (Figure 14), the sequence from the tentacle of a known *Chrysaora fuscescens* medusa grouped within the *Chrysaora* genus, depicting a monophyletic clade. The distance tree, however, did not depict monophyly (Figure 15). A direct comparison of tentacle sequence to another *C. fuscescens* sequence could not be made because GenBank does not have a COI sequence on file for this species.

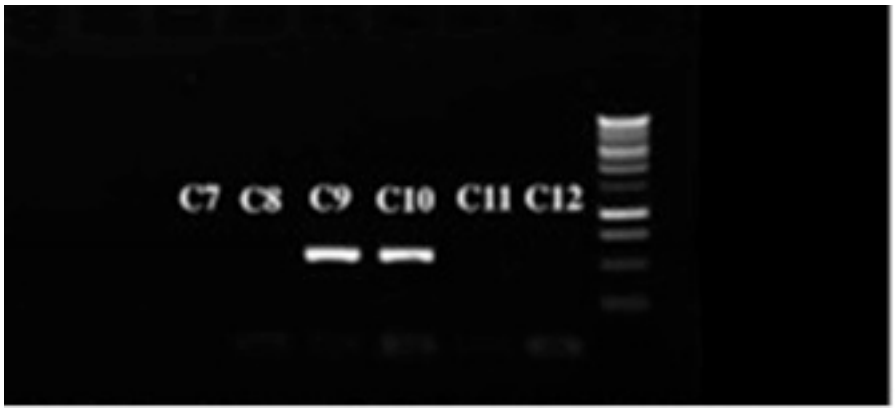

Figure 10. DNA quantification of PCR products using diluted samples on 1% agarose gel. From left to right: C7 & C8: replicates of scyphistoma sample 1 with 1 ul 1/10th dilution of sample, 19ul Master Mix (MM), and the LCOjf/HCOcato primers; C9 & C10: replicates of tentacle 1ul of sample, 19 ul MM, and the LCOjf/HCOcato primers; C11 & C12: replicates of scyphistoma sample 2 with 1ul of sample, 19ul MM, and the LCOjf/HCOcato primers.

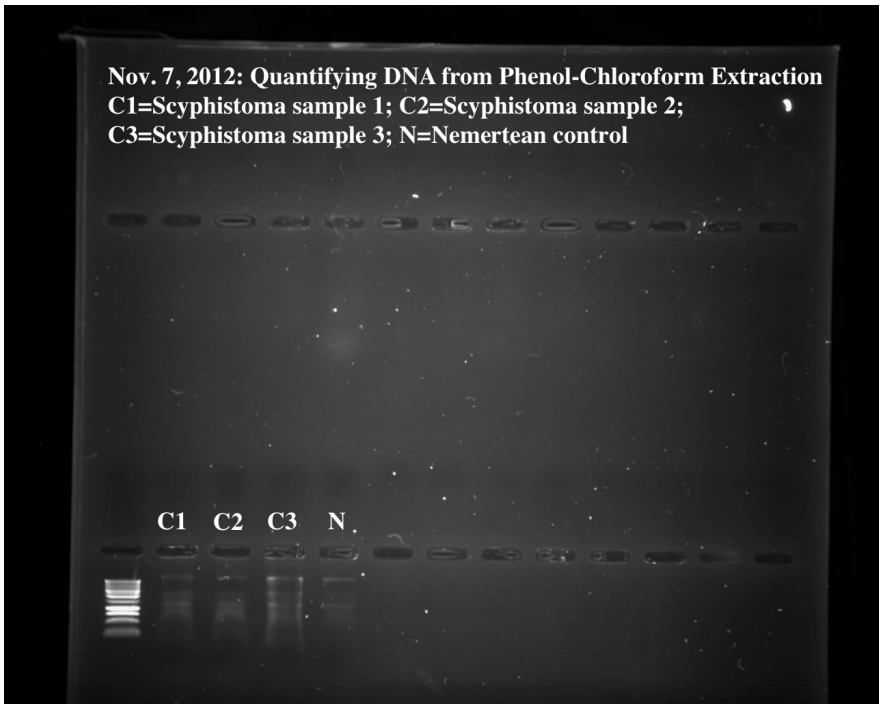

Figure 11. Electrophoretic analysis of DNA extracted from Charleston Marina scyphistomae and nemertean control on 1% agarose gel.

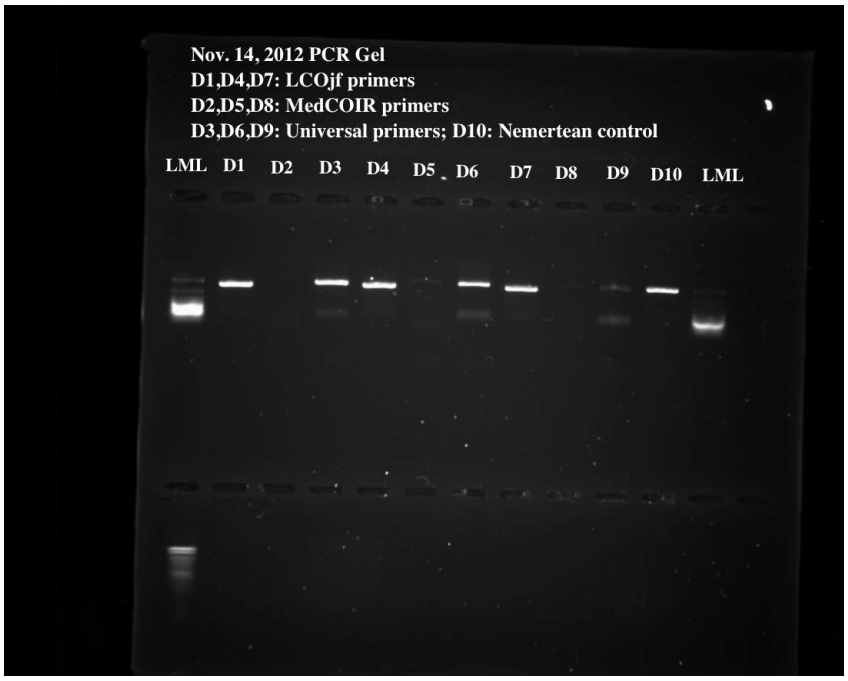

Figure 12. PCR amplification results verified on 1% agarose gels showing bright bands for LCOjf primers, failed bands for MedCOIR primers, and successful, bright bands for universal primers.

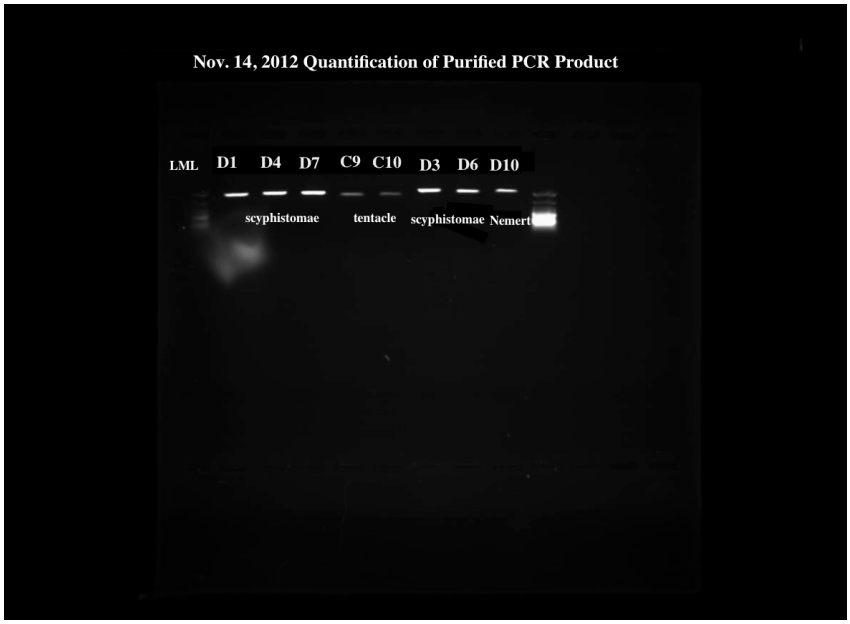

Figure 13. Purified PCR products of scyphistomae, *Chrysaora fuscescens* tentacle, and nemertean control. Electrophoresis was preformed on 1% agarose gel and stained with ethidium bromide. From left to right: Low Mass Ladder (LML); PCR products from three scyphistomae obtained with the scyphozoan-specific primers LCOjf/ HCOcato; two PCR products from *Chrysaora fuscescens* tentacle tissue with the LCOjf/ HCOcato primers; one nemertean control tissue with the CO1dr/ LCO1490 primers.

Table 5. Identified sequences from NCBI BLAST program.

Sequence Name	Organism collected	Primer Pair	Closest match	Query coverage	Identity	E-value	Taxonomy of closest match
1DF_R	Scyphistoma 1	LCOjf/ HCOcato	*Aurelia labiata*	100%	100%	0.0	Cnidaria; Scyphozoa
3DF_R	Scyphistoma 1	LCO1490/ HCO2198	*Eupolymnia heterobranchia*	100%	99%	0.0	Annelida; Terebellidae
4DF_R	Scyphistoma 2	LCOjf/ HCOcato	*Aurelia labiata*	100%	100%	0.0	Cnidaria; Scyphozoa
6DF_R	Scyphistoma 2	LCO1490/ HCO2198	*Balanus glandula*	100%	99%	0.0	Arthropoda; Cirripedia
7DF_R	Scyphistoma 3	LCOjf/ HCOcato	*Aurelia labiata*	100%	100%	0.0	Cnidaria; Scyphozoa
9CF_R	*C. fusescens* tentacle	LCOjf/ HCOcato	*Halecium halecinum*	92%	81%	2e-108	Cnidaria; Hydrozoa

Table 6. Taxonomy and GenBank Accession Numbers for reference scyphozoan sequences analyzed in this study.

Order	Family	Genus	Species	Accession Number
Coronatae	Atollidae	*Atolla*	*tenella*	GQ120084.1
Semaeostomea	Ulmaridae	*Aurelia*	*aurita*_1	HM053519.1
Semaeostomea	Ulmaridae	*Aurelia*	*aurita*_2	JQ623914.1
Semaeostomea	Ulmaridae	*Aurelia*	*labiata*_newport	AY903074.1
Semaeostomea	Ulmaridae	*Aurelia*	*labiata*_tomales	AY903075.1
Semaeostomea	Ulmaridae	*Aurelia*	*limbata*	AY903189.1
Semaeostomea	Ulmaridae	*Aurelia*	sp.1	AY903202.1
Semaeostomea	Ulmaridae	*Aurelia*	sp.1-tokyo	AY903206.1
Semaeostomae	Pelagiidae	*Chrysaora*	sp. JSL	EU439431.1
Semaeostomea	Pelagiidae	*Chrysaora*	*melanaster*	FJ602545.1
Semaeostomea	Pelagiidae	*Chrysaora*	sp.MD	DQ083524.1

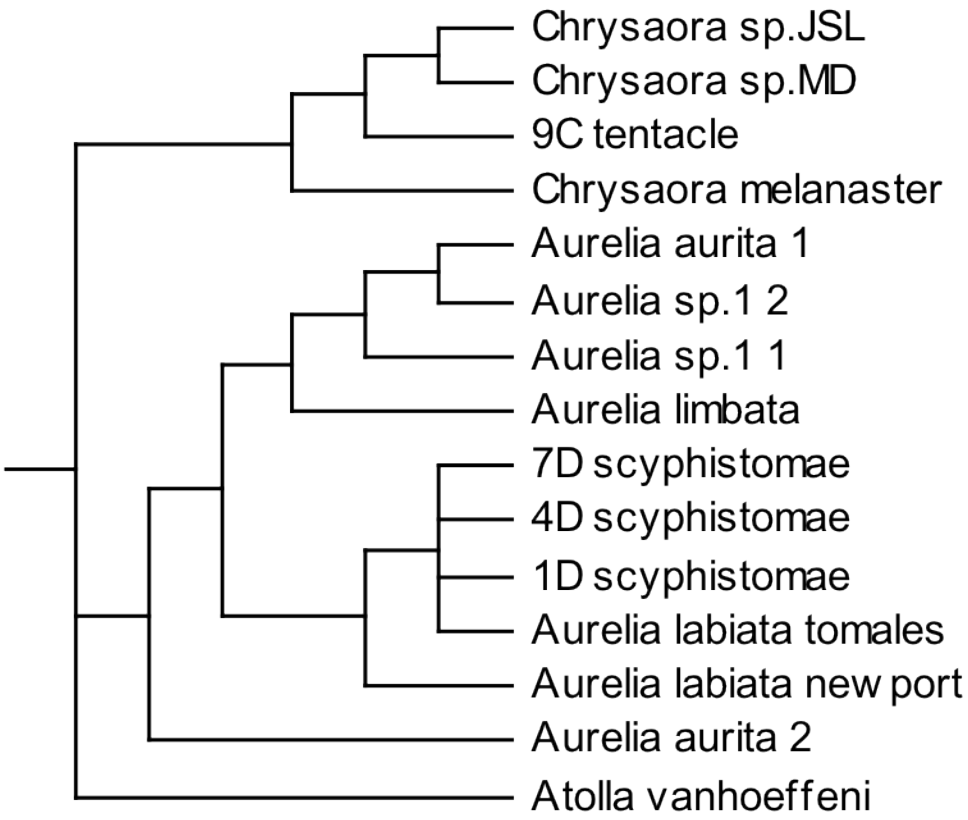

Figure 14. Maximum Parsimony Tree produced from COI gene sequences extracted from scyphistomae tissue samples, one known *Chrysaora fuscescens* tentacle sample, and sequences downloaded from GenBank. Tree developed using PAUP. *Atolla vanhoeffeni*, a coronate scyphozoan, is the outgroup. Sample abbreviations are the same as in Table 4.

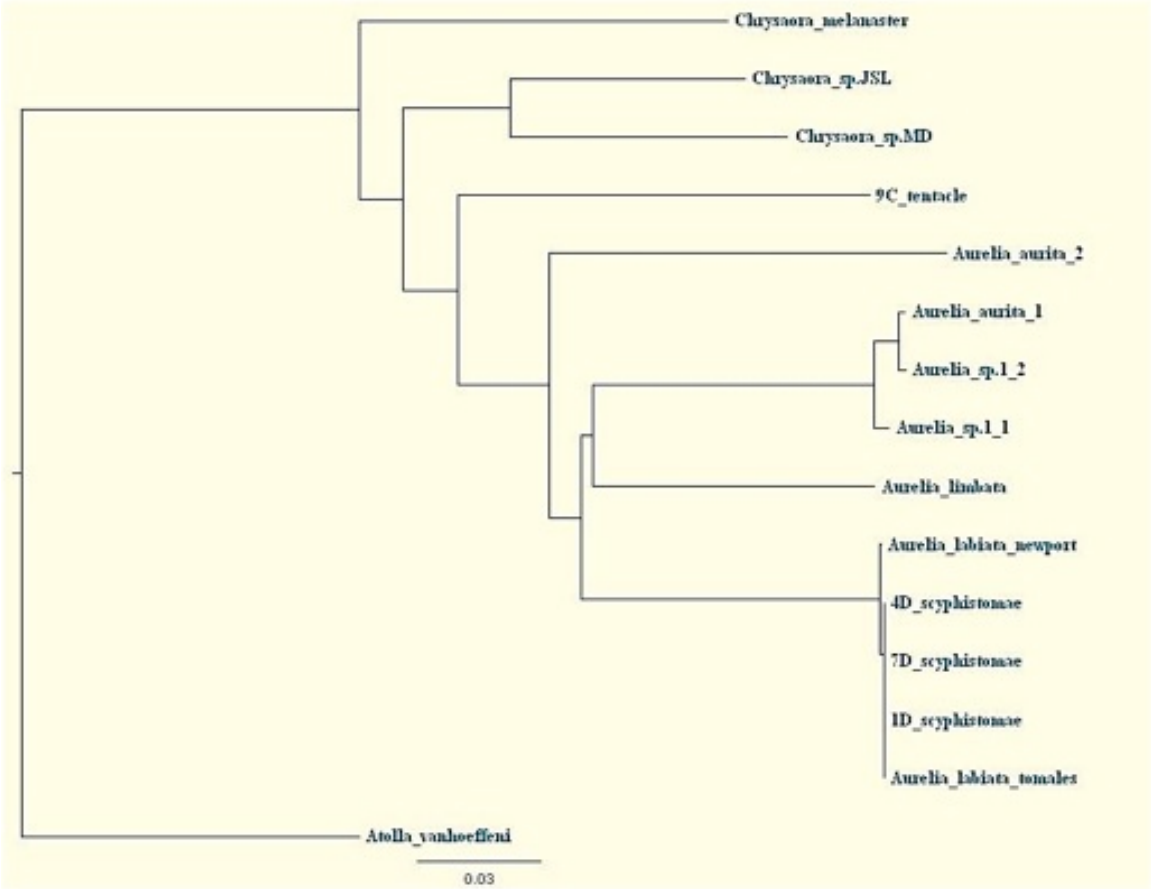

Figure 15. Distance tree produced from COI gene sequences extracted from scyphistomae tissue samples, one known *Chrysaora fuscescens* tentacle sample, and sequences downloaded from GenBank. Developed using FigTree v.1.3.1. *Atolla vanhoeffeni*, a coronate scyphozoan is the outgroup. Sample abbreviations are the same as in Table 4.

Discussion

According to Mills and Larson (2007), "…the soft, white 'scyphistoma' stage…can be encountered in great numbers under shaded parts of floats in harbors or marinas or on boat hulls. Most (probably all) of these scyphistomae encountered on the West Coast of America belong to *Aurelia*" (p. 168). We initially suspected that the scyphistomae in the Charleston Marina may belong to *Chrysaora fuscescens* because an ephyra had been collected in a plankton tow there (Brush and Sutherland, unpublished

data). Using the "barcoding" region of the Cytochrome Oxidase subunit I gene, we identified the scyphistomae in the Charleston Marina as belonging to *Aurelia labiata.*

In 2001 the *Aurelia labiata* species complex was resolved through morphological analysis of its enlarged manubrium and canal system (Dawson and Martin, 2001; Gershwin, 2001). Although *A. labiata* lacks the morphological diversity of *A. aurita*, the species still encompasses a distinct southern, central, and northern morph, which may represent separate species (Dawson, 2003; Gershwin, 2001). Our scyphistomae sequences match the central morph that ranges from Santa Barbara, California, to Oregon (Gershwin, 2001).

This study highlights a methodological aspect of working with scyphistomae. Our two attempts to extract DNA from scyphistomae using a standard column-based method (Qiagen's DNeasy Blood and Tissue Kit) did not produce DNA of sufficient quantity or quality for PCR, though it did work for scyphozoan medusa stage tentacles. However, we succeeded in extracting DNA from scyphistomae using a phenol-chloroform based method. This is likely attributable to the nature of the tissue. This is consistent with previous findings that phenol–chloroform extraction protocol yields significantly more DNA than column-based methods (e.g. DNeasy kits) for Cnidarian tissue (e.g. Gaither et al., 2011) and scyphistomae in particular (Pinto et al., 2000). *Aurelia* DNA may be particularly susceptible to degradation—perhaps because of a greater concentration of catalytic enzymes (Dawson et al., 1998).

We also found that the universal COI primers (Folmer et al., 1994) did not work well for *Aurelia*. PCR reactions conducted with these primers instead amplified contaminant DNA (a barnacle *Balanus glandula* and a terebellid polychaete *Eupolymnia*

heterobranchia). Contamination of samples likely happened during collection of samples. We scraped the scyphistomae from under the docks using a makeshift hoe; this method evidently captured tissue from other invertebrates in the fouling community of these docks. Using scyphozoan-specific primers (Dawson and Jacobs 2001), we successfully amplified the COI gene region from the scyphistomae.

The source locations of *Chrysaora fuscescens* polyps therefore remain unknown. Mature medusae of *C. fuscescens* are most abundant in nearshore waters proximate to jetties and bays, suggesting that the polyps are either attached to hard estuarine substrates akin to *A. labiata* polyps, or instead colonize the underhangs of rocky shelf reefs (Suchman and Brodeur, 2005). Although we did not sample exhaustively, we do not believe that *Chrysaora* scyphistomae co-habit with *Aurelia* polyps in the Marina for three reasons. The first is that laboratory experiments conducted after this study began show that *C. fuscescens* planulae are strongly averse to concrete—the substrate underneath the docks (Conley, this thesis). Second, it is improbable that the polyps are on other parts of the docks, since the remaining dock structures are vertical, and planulae almost exclusively prefer to settle on horizontal undersurfaces as opposed to settling vertically or upright (Arai, 1997; Conley, this thesis). Third, *Aurelia aurita* scyphistomae readily consume planulae of other species to avoid interspecific competition (Gröndol, 1988). It is also improbable that polyps are elsewhere in the estuary, such as oyster "reefs," because oyster biologists and culturists have never observed them (Vern Simmons, Umpqua Oysters, personal communication, Dec. 6, 2012; C. Langdon, Oregon State University, personal communication, Oct. 31, 2012; A. Shanks, University of Oregon, personal communication, April 9, 2012).

The polyps of *Chrysaora pacifica*, a close congeneric of *C. fuscescens*, were recently discovered on stones and the dead shells of the clam *Meretrix lamarckii* within 5 meters depth of the Sagami Bay, Japan (Toyokawa, 2011b). The polyps of *C. pacifica* preferred to settle on the concave surface of bivalve shells or in hollows of the stones (Toyokawa, 2011b). Although *C. fuscescens* planulae are capable of settling on both *Crassostrea gigas* and *Ostrea lurida* shells in the laboratory, they prefer to settle in the pockmarks of the undersides of rock (Conley, this thesis). Since we failed to locate *C. fuscescens* polyps on estuarine structures close to where the ephyrae are found, our results suggest that it may be more productive to search for *C. fuscescens* polyps on rocky reefs or the interstices of jetty rocks rather than on floating docks.

CHAPTER IV

SOCIOECONOMIC IMPACTS OF JELLYFISH ON FISHERS IN THE NORTHERN CALIFORNIA CURRENT

Introduction

The California Current System (CCS) extends from Cape Mendocino, California, to the northern tip of Vancouver Island and comprises the eastern portion of the Central Pacific Gyre (Field et al., 2006). Major physical promontories along this stretch include Point Conception, Cape Mendocino and Cape Blanco. The Northern Current transports relatively cool and fresh waters offshore and into the Southern California Bight, while the Southern Undercurrent transports warm and saline waters onshore (Bograd and Lynn, 2003). This circulation pattern greatly impacts primary and secondary production, and the biological richness of this boundary current system supports numerous commercial fisheries and hundreds of coastal communities (Field et al., 2006; Sepez et al., 2006).

The CCS has witnessed substantial declines in fishing pressure since the 1990s and biomass has increased above the long-term average, in large part due to area closures, gear and effort restrictions, and new approaches to catch allocation and enforcement (Worm et al., 2009). The shelf, however, still remains heavily fished—sustaining a mixed-stock groundfish fishery, much of the Pacific whiting (*Merluccius productus*) fishery, salmon (*Oncorhynchus tshawytscha* and *O. kisutch*) fisheries, sardine (*Sardinops sagax*) fishery, and mackerel fisheries (both *Trachurus symmetricus* and *Scomber japonicus*) (Field et al., 2006). Collectively, the commercial fisheries in the CCS sustain 125 communities in the Pacific region, annually contributing over $28 billion in seafood

sales (National Marine Fisheries Service 2010).

Recent studies have found evidence of a pervasive jellyfish proliferations in coastal regions (Brotz et al., 2012), and in some areas, these have disrupted fisheries. For example, blooms of *Nemopilema nomurai* in Japan in the early- and mid-2000s clogged and burst set-nets, eliciting complaints from over 100,000 commercial fishers (Kawahara et al., 2006; Uye, 2008). Blooms of *Stomolophus meleagris, Aequorea* sp., and *Cyanea* sp. clogged fishing nets and reduced catches in the East China Sea and Yellow Sea (Cheng et al., 2005). More recently, employees of fish factories in Peru reported that 387.4 tons of Peruvian anchovy (*Engraulis ringens*) were discarded during the study period of 35 days because bycatch of *Chrysaora plocamia* exceeded 40% of total landings (Quiñones et al., 2012). Jellyfish may also sting juvenile fish, producing severe lesions that reduce the commercial value of the fish, or even causing mass mortalities (e.g. Bämstedt et al., 1998).

In the CCS, the feeding preferences of medusae have high trophic overlap with planktiverous fishes (e.g. Brodeur et al., 2008). Euphausid eggs comprise the majority of *Chrysaora fuscescens* and *Aurelia labiata* prey consumption, and the medusae therefore compete for a common food source with Pacific sardine (*Sardinops sagax*), Pacific saury (*Cololabis saira*), Northern anchovy (*Engraulis mordax*), and Pacific herring (*Clupea pallasi*). The hydromedusa *Aequorea victoria* almost exclusively consumes *C. pallasi* larvae when the larvae first hatch (Purcell, 1989; Purcell and Grover, 1990). Within the Oregon inner-shelf ecosystem in late summer, jellyfish surpass forage fish as zooplankton consumers, and may divert zooplankton production away from upper trophic levels (Ruzicka et al., 2007).

Jellyfish population dynamics in the Northern California Current are governed in part by physical forces; the abundance of large medusae is positively correlated with upwelling from the "cool phase" of the Pacific Decadal Oscillation as well as higher salinities resulting from reduced streamflow (Suchman et al., 2012). Blooms in Oregon and Washington reach highest numbers in late summer and tend to be concentrated around headlands and capes (Suchman et al., 2012). Ultimately, the benthic polyp stage is the primary contributor to seasonal and annual population variation of the adult medusae, and little information exists on scyphistomae populations in the CCS. Long-term data sets on medusae density in Southern California show significant increases (CalCOFI, 2010), and anecdotal evidence suggests jellyfish populations along the Central California coast also may be increasing (Brotz, 2011).

Cruise surveys, aerial surveys, and acoustic back-scatter techniques indicate that jellyfish in the waters along Oregon's coast bloom seasonally in a density suspected to be sufficient to negatively impact fishing activities. Biomass of *C. fuscescens* was documented to reach 50 mg C/m^3 in 1981, 64 mg C/m^3 in 2000, and 28 mg C/m^3 in 2002 (Graham, 2009; Shenker, 1984; Suchman and Brodeur, 2005). Comparatively, densities of the blooms of *N. nomurai* that burst the nets of Japanese fishers were 40.5 mg C/m^3 (Lucas et al., 2011; Uye, 2008). Since economic impact analyses have to date been conducted only for anomalous, high-density blooms, data from fishers in the CCS may serve as a useful baseline from which to determine the "average" socioeconomic impact jellyfish blooms cause fishers.

Salmon trolling, in particular, is a highly variable industry on which many coastal Oregon communities depend. Although there are some reasons for optimism regarding

salmon populations—namely that Chinook salmon landings have increased over the long term, albeit at the expense of Coho salmon (Schindler, 2011)—this does not necessarily translate to increased revenues for salmon trollers. Even though some stocks are rebounding, the real per pound ex-vessel price for salmon continues to decline, primarily because of cheaper farmed salmon that has transformed the market to the detriment of capture fishers (Anderson, 2002; Irvine et al., 2009; Naylor et al., 2003). As Noakes and Beamish (2011) describe, "While Pacific salmon catch and overall abundance are generally good at this time, the economic health and stability of commercial salmon fisheries is less positive…In its present configuration and without significant subsidies, the North American commercial salmon fishery will continue to experience significant distress from an economic perspective" (p. 32-33). All commercial fishers face the economic pressures of increased fuel costs, annual boat depreciation, variable operating costs and landings value (Lam et al., 2011; Sumaila et al., 2008). Many commercial fisheries are therefore perched in a potentially precarious economic position, where jellyfish may further increase the cost of fishing effort.

Chrysaora fuscescens is the most abundant semaeostome in the northeast Pacific whose blooms reach the greatest density (Suchman and Brodeur, 2005). Salmon trolling—both for Chinook and Coho salmon—occurs in high overlap with the spatial distribution of *C. fuscescens,* occupying surface waters within the inner shelf, primarily in cold upwelled waters (Brodeur et al., 2008). Therefore, in this study uncovering the impact of jellyfish on salmon trollers was a priority, but it also sought to collect baseline data on the type and magnitude of economic damages caused by jellyfish on multiple fisheries in the region. I simultaneously assessed fishers' perceptions of jellyfish

population trends in the Northern California Current and sought to determine the degree to which jellyfish reduce or otherwise affect fish capture.

Methods

On September 25, 2012, surveys were mailed to resident commercial shrimpers, salmon trollers, and rockfish (black, blue) fishers registered in the Oregon Department of Fish & Wildlife database of permit holders (n=761), and groundfish limited-entry permit holders registered in the Northwest Pacific Management Council database (n=131).

Fishers were asked to estimate the indirect damages caused by jellyfish—including costs of relocating to avoid blooms, lost fishing time, time lost to bycatch sorting, fish depreciation, and gear damage. In an attempt to account for differences in average revenue between vessels, cost estimates were requested both as a numerical value and as a percentage of seasonal revenue. The nuisance level of jellyfish to fishing activity and the frequency and severity of jellyfish stings was also evaluated using ranking questions. Fishers were asked whether they had observed a noticeable change in jellyfish populations over the past five years by rating the statement "I see more jellyfish during my fishing now than I did five years ago" using a Likert scale. Fishers were asked to identify jellyfish to species-level in a multiple-response question using color photographs for reference (Figure 27). To analyze the nuisance level associated with different jellyfish species, the nuisance level reported by each respondent was assigned to each of the one or more species indicated in the multiple-response question.

To assess nuisance level by fishing location, a weighting system was used according to how many regions in which fishers' reported fishing (Nagata et al., 2009). Fishing regions within the CCS were divided based on physical promontories of the

coastline (Figure 16), with "North of Columbia River" considered one macro-scale region and "South of Oregon" another region. Regions within Oregon were examined at the meso-scale (e.g. Columbia River to Cape Falcon; Cape Arago to Cape Blanco). Some respondents reported fishing in a localized area (e.g. Winchester Bay) while others reported fishing the entire coastline. Therefore, to equalize the weight of the answers in the analysis, each answer was attributed a weight of 1, and this value was then divided by the total number of locations indicated in the survey. Thus, when only one fishing location was reported, a weight of 1 was attributed to this response; when two locations were reported, the weight was 0.5, and so on; the maximum number of locations indicated was eight (constituting the entire coastline from Washington to California) up, and each corresponding location-nuisance level received a weight of 0.125. This method assumes spatial homogeneity of nuisance level reports based on the respondents' respective fishing area(s).

Figure 16. Study area of survey respondents' fishing locations in the California Current System.

Results

One-hundred seventeen survey responses were received, representing fishers across the Pacific region of North America, but the majority of responses came from salmon trollers (Table 7) concentrated in Oregon (Table 8). Winchester Bay was the

location with the highest median nuisance level, while Rogue Canyon and the Cape Blanco environs had the lowest nuisance level (Table 8). Fishers in central Oregon purportedly experience higher nuisance from jellyfish than fishers to the north or south (Figure 17). While results from the surveys indicated considerable differences in nuisance (Figure 18) and economic impact (Table 7) from jellyfish among fisheries, some commonalities existed across gear types. Fishers revealed that the social impacts of jellyfish tend to be minimal compared to economic ones: the majority (n=54) reported never experiencing jellyfish stings during their fishing, or only being stung once every few months in peak jellyfish season (n=22). Those infrequent stings are reportedly associated with only mild pain (Figures 19, 20). Five fishers reported wearing gloves as a simple, effective remedy for preventing stings.

Eighty-three percent of respondents who reported that jellyfish were a nuisance were able to identify the jellyfish to species-level using the color photographs provided in the mailed survey. Fifty-three fishers were able to pinpoint a precise year(s) in which they recalled observing the highest jellyfish abundance ($mode = 2011; n = 52$) (Figure 21). Collectively, fishers did not report a noticeable change in jellyfish population trends in their respective fishing locations (Figure 22). Fishers frequently reported that while jellyfish often do pose a nuisance to their fishing and often increase their workload, it is extremely hard to quantify a revenue loss for many of the ways jellyfish force fishers to modify their work. Several fishers (n=20) reported never having thought about jellyfish as a form of revenue loss before, but that jellyfish did increase labor. Fifty-nine percent of respondents reported that jellyfish do affect their revenue. The species predominantly responsible for these losses was *Chrysaora fuscescens*, followed by *Aequorea* sp. (Figure

23), but different species accounted for nuisance across the different fisheries (Figure 24). *C. fuscescens* was the species associated with the greatest frequency of high-nuisance (≥ 3 on a 1-to-5 ranking scale) reports (Figure 25).

Some sample quotes are provided here in an attempt to represent the 41% of respondents who reported that jellyfish do not impose economic losses on their fishing:

- *I am a salmon troller and avoid areas thick with jellyfish but it does not affect my income. I have just as much chance of catching in 'clean water.'*
- *Don't really know what jellyfish are in the ocean, but hear some fish eat them… I wear gloves most of the time while fishing. However I do take them off to get all the jellyfish off my lures. They don't seem to bother my hands.*
- *I incur very little loss due to jellies. They are just a nuisance to keep off your gear. Sometimes they are bad enough to relocate but rarely stop me from fishing.*
- *In the 70s we had a tow with so many we couldn't get them off the boat. That was back when we were beach dragging. We do not trawl now days.*
- *Trolling for salmon, sea nettles foul gear. Only more work and nuisance.*
- *I troll for salmon and usually avoid fishing where jellies are present, usually nearshore. Sometimes you have to fish where there are jellies, but they are rather a nuisance than a deterrent to income and by wearing gloves, avoid the minor discomfort of being stung.*
- *Haven't seen the purple sail swarms I used to see, and sunfish populations have been increasing but don't see many of the really big ones anymore (all they eat is jellyfish).*
- *Usually more in California. Money lost is hard to determine. Extra work to clean off wire. Change leaders more often because of buildup. Unable to fish in large areas. Not much time in California available in last 7 years. Have had to pull gear and relocate in past. Very little in 2012 from Point Arena north.*

Table 7. Summation of jellyfish impacts on different fishing gear types in the Northern California Current. Economic impacts calculated using precise values provided by respondents. Qualitative estimates such as "some," "small amount," and "unknown" were omitted from this analysis. One rockfish fisher reported losses of "$50 per day when fish are around," which was conservatively calculated as $50. Because fishers were allowed to select multiple species of nuisance jellyfish and multiple forms of jellyfish impact, *n*-values for these columns include double-counts and therefore may total to more than the total respondents for that gear type.

Gear type	**Jellyfish species that pose nuisance** (in ranked order)	**Predominant form of impact** (number of reports)	**Seasonal revenue loss 2012** ($\mu \pm$ std. error)
Salmon/tuna troll (n=87)	*Chrysaora fuscescens, Cyanea capillata*, *Aurelia labiata, Aequorea* sp., *Phacellophora camtschatica*, *Periphylla periphylla*	Foul gear (49), relocate (34), reduce catch (15), shorten fishing time (8)	$1,010 ± 280
Pink shrimp trawl (n=8)	*Aequorea* sp., *Aurelia labiata*, *Vellela vellela*	Relocate (6), plug web and reduce vessel speed and catch (3), shorten fishing time (2)	$10,000 ± 5,305
Rockfish hook & line (n=8)	*Chrysaora fuscescens*	Reduce catch (1)	$105 ± 100*
Groundfish trawl (n=5)	*Chrysaora fuscescens*	Relocate (1), shorten fishing time (1), foul gear (1), bycatch increases sorting time (1), changes fishing practices (1)	$231 ± 250
Crab pots (n=13)	*Chrysaora fuscescens*, *Aurelia labiata, Vellela vellela, Cyanea capillata*	Stung (5); stung in eyes (4); foul pot lines when retrieving (6); Relocate (3)	N/A
Sardine seine (n=1)	*Aurelia labiata*	Relocate (1)	Unknown

Table 8. Frequency table showing nuisance level of jellyfish to different fishing locations in the Northern California Current. Species accounting for nuisance: CF=*Chrysaora fuscescens*; AQ=*Aequorea* sp.; AL=*Aurelia labiata*; CC=*Cyanea capillata*; PC=*Phacellophora camtschatica*; VV=*Vellela vellela*; UI=Unidentifiable. Numbers under each species indicate the number of reports that this species was a nuisance. If a single respondent reported multiple species, each species was counted separately. *N* indicates number of respondents who reported fishing in the respective location. Offshore locations (indicated by a *) are double-counts from respondents categorized within a nearshore region, since all but one of the respondents who reported fishing offshore also fished in coastal locations.

		Species							
Location	Nuisance level (median)	CF	AQ	AL	CC	PC	VV	UI	*N*
Winchester Bay	4.5	2	1	0	0	0	0	0	2
Falcon to Arago	4	1	0	0	1	0	0	0	1
Perpetua to Arago	3	4	2	1	0	0	0	3	9
Falcon to Blanco	3	1	0	0	0	0	0	0	1
Columbia to Foulweather	3	2	0	0	0	0	0	0	3
Arago to Blanco	3	3	5	2	0	0	1	0	9
Foulweather to Perpetua	2.5	9	1	1	4	1	0	0	8
Columbia to Falcon	2.5	1	0	0	0	0	0	1	2
Coquille Bank*	2.5	1	2	3	1	1	0	0	5
South of Oregon	2	6	0	2	0	0	0	0	8
Perpetua to Blanco	2	3	0	0	1	0	1	2	7
North of Columbia River to Foulweather	2	2	0	0	1	0	0	0	3
Falcon to Perpetua	2	4	0	0	2	0	0	0	5
Falcon to Foulweather	2	9	1	0	1	0	2	1	13
Entire coast	2	5	2	0	0	0	0	0	6
Columbia to Perpetua	2	2	0	0	1	0	0	0	2
Stonewall Bank*	2	10	2	0	2	0	2	2	15
Heceta Bank*	2	8	4	1	2	0	2	2	15
Arago to state line	1.5	1	0	2	1	1	0	0	2
Perpetua to state line	1	0	1	1	0	0	0	0	1
Perpetua to south of Oregon	1	0	1	0	0	0	0	1	3
North of Columbia River to Falcon	1	0	0	0	0	0	0	1	1
Foulweather to south of Oregon	1	0	1	1	0	0	0	0	1
Foulweather to Arago	1	2	0	0	0	0	1	1	3
North of Columbia River	0.5	0	1	1	0	0	0	1	5
Astoria Canyon*	0.5	1	0	0	0	0	0	0	2
Rogue Canyon*	0	0	0	0	1	1	0	0	2
Blanco to state line	0	3	0	1	1	0	0	0	11
Blanco to south of Oregon	0	1	0	0	0	0	0	1	2
Arago to south of Oregon	0	1	1	1	0	0	0	0	0

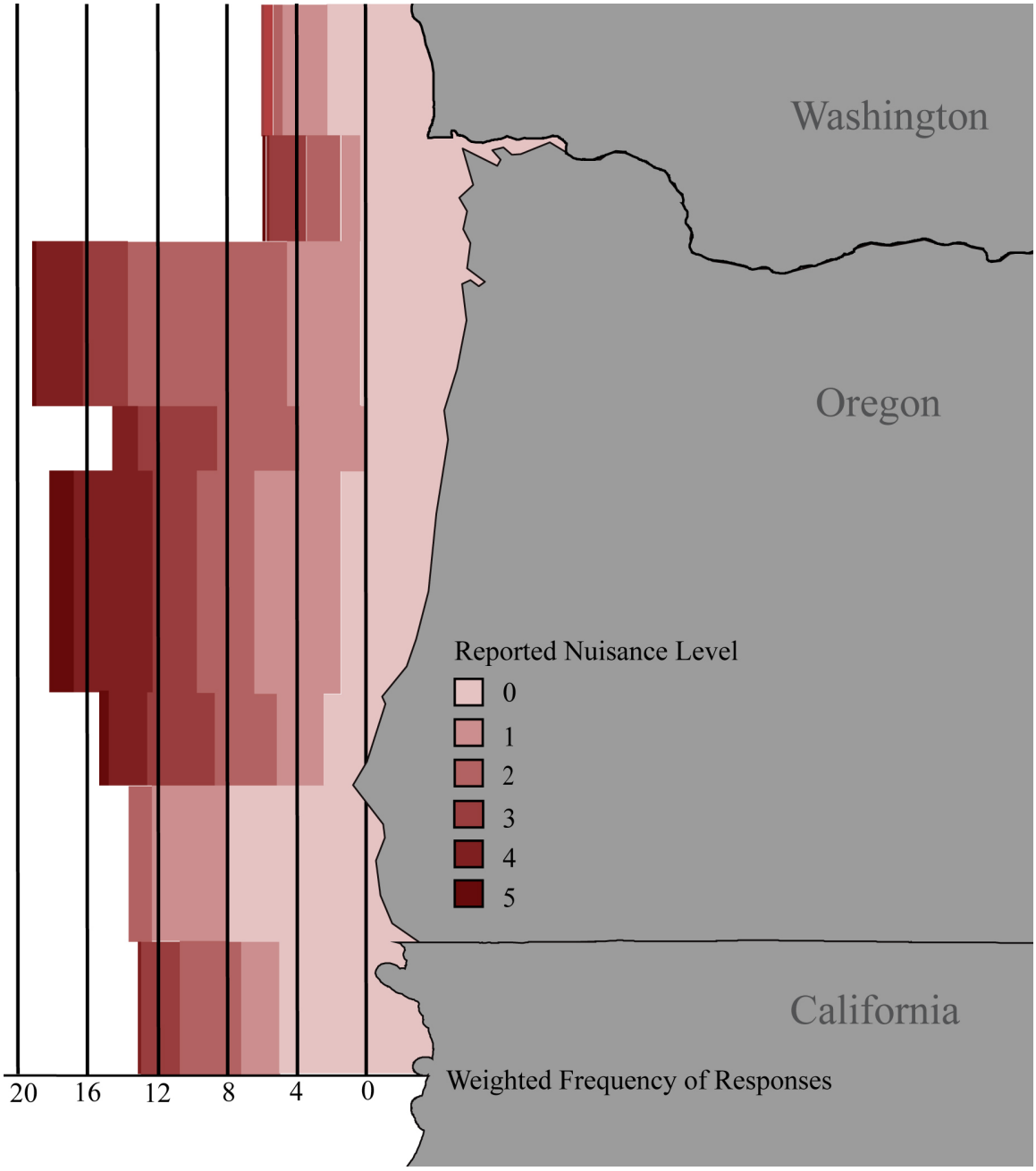

Figure 17. Map of California Current System showing the frequency and nuisance level of jellyfish by fishing location. Fishing regions correspond to those shown in Figure 16. Oregon fishing regions are divided based on physical promontories of the coastline (e.g. Cape Blanco to Cape Arago constitutes one region); data from Washington and California are examined at the state-scale. These regional divisions only consider fishers' longitude, not latitude. The x-axis shows frequency of responses, weighted according to how many regions in which fishers' reported fishing.

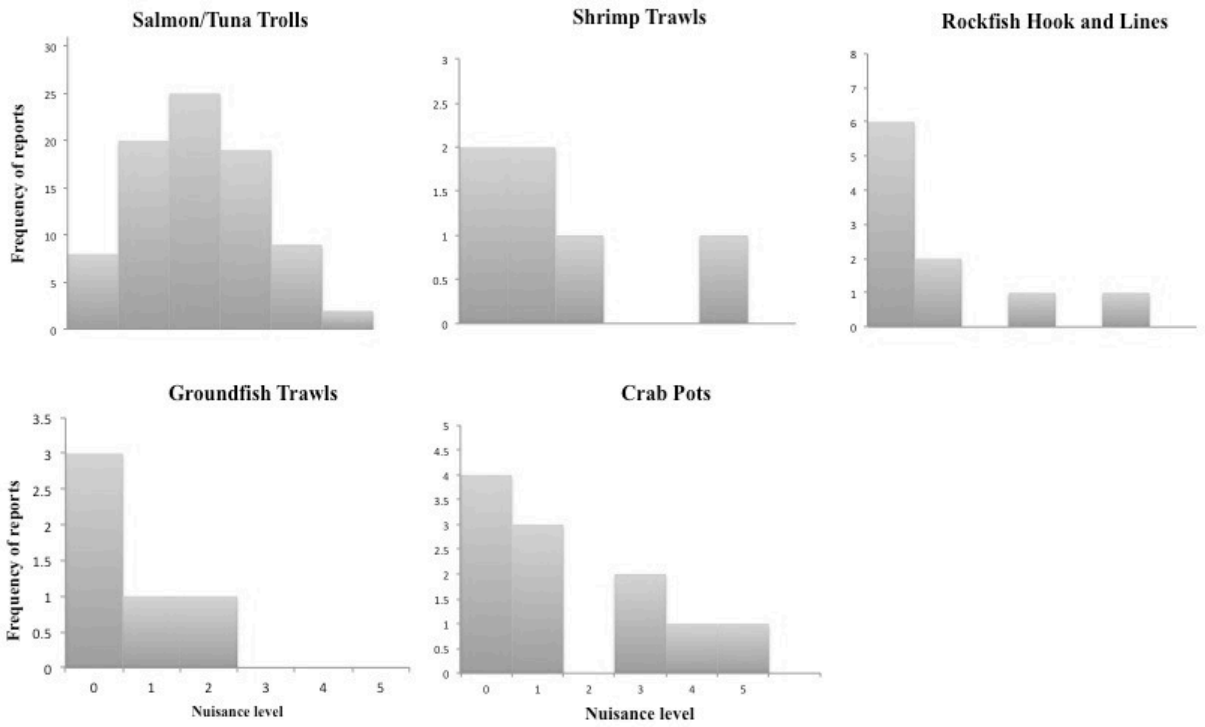

Figure 18. Histograms of jellyfish nuisance level among fishing gear types in the Northern California Current. Nuisance level is ranked on a 0-5 scale with "0" corresponding to no nuisance and "5" to severe nuisance. Developed using StatPlus:mac LE.

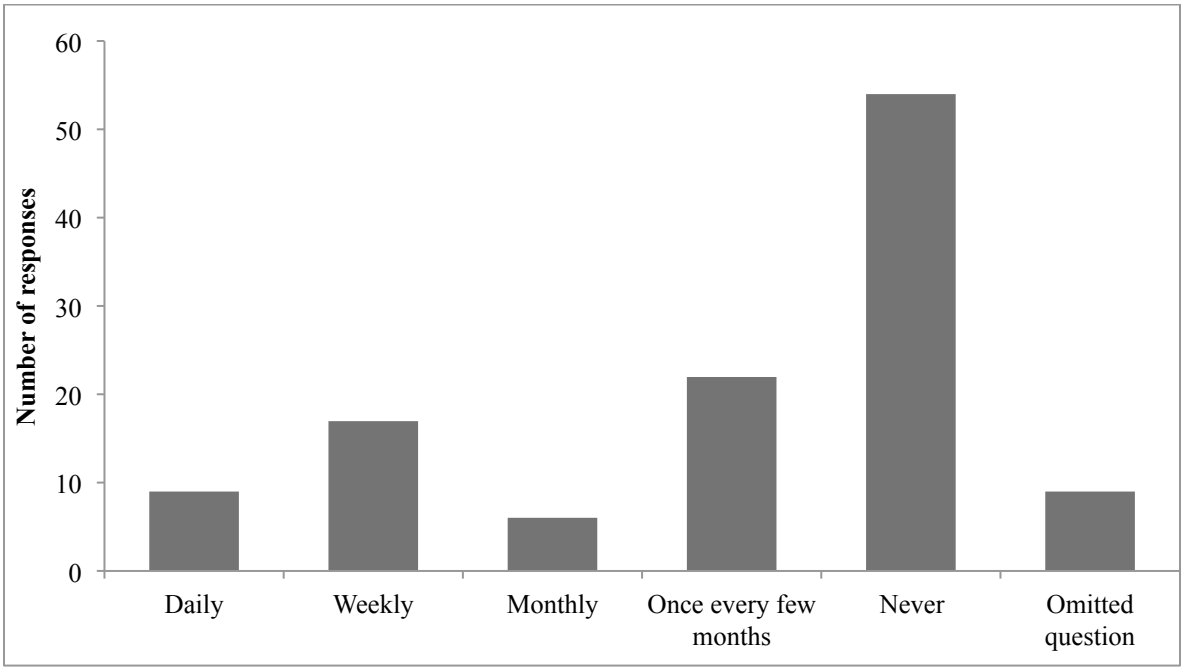

Figure 19. Fishers' assessment of frequency stung by jellyfish while fishing June-September (n=117).

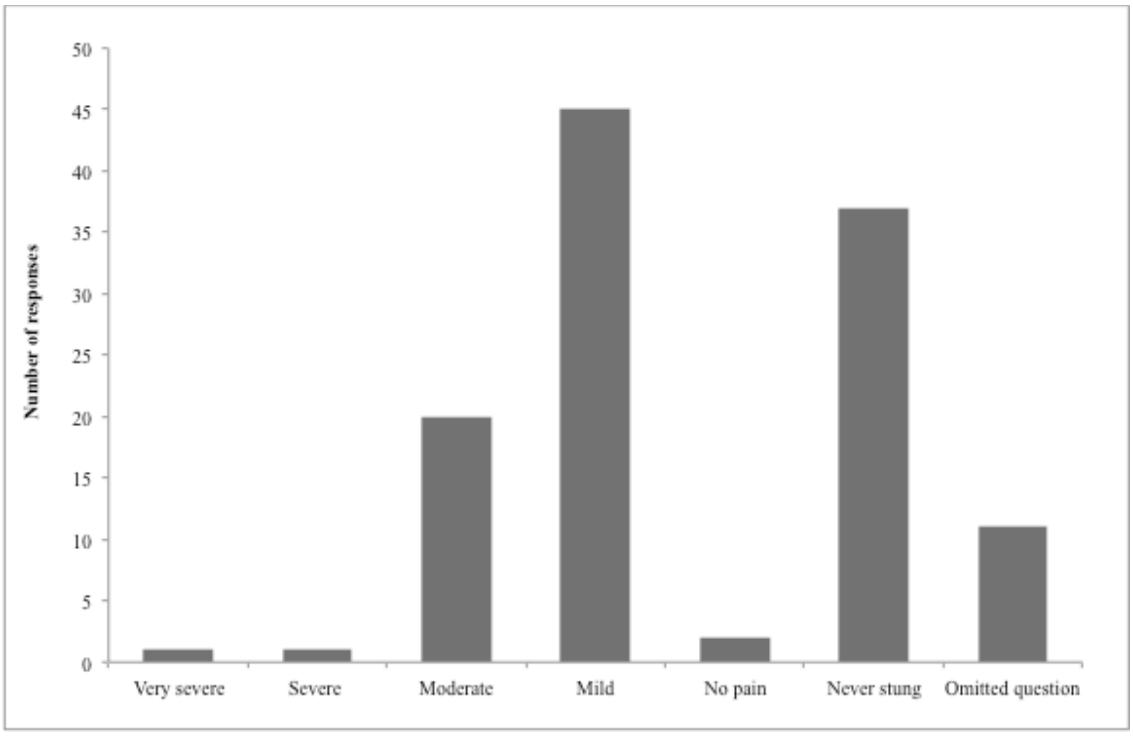

Figure 20. Fishers' assessment of pain caused by jellyfish stings (n=117).

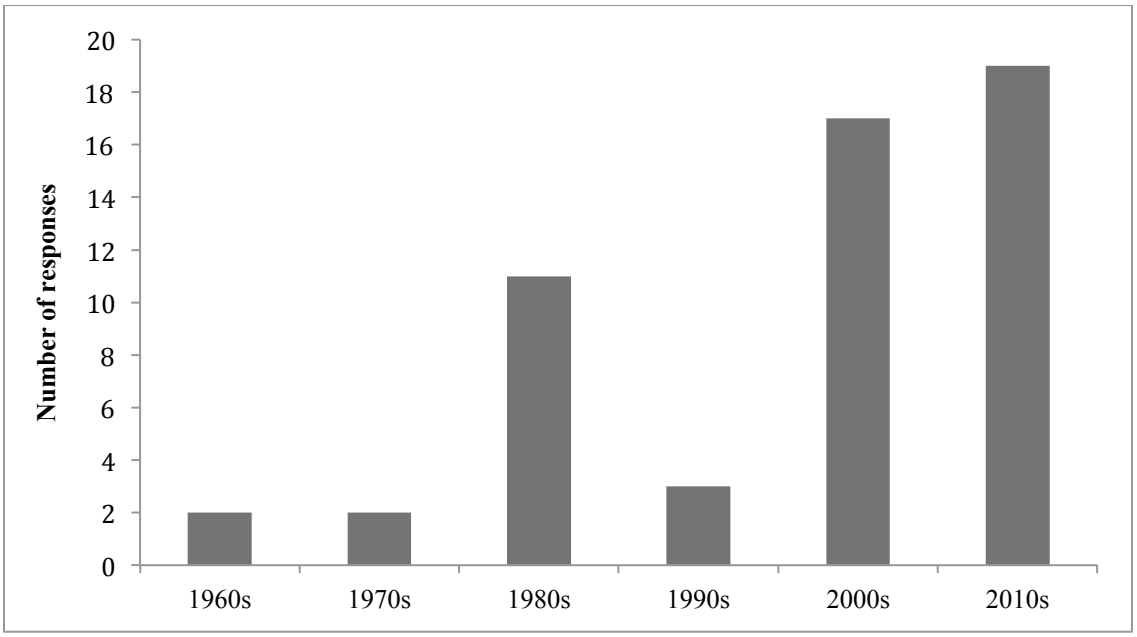

Figure 21. Respondents' reports of year(s) with maximum jellyfish abundance (n=52). Respondents who reported a range of years (e.g. 2009-2011) were assigned to the closest corresponding decade. One respondent who reported high abundance in El Nino years was excluded from the analysis. Two respondents reported two different years in different decades, and each of these responses was counted separately, for a total of 54 observations. Decadal intervals were selected because of evidence that jellyfish populations fluctuate decadally (Condon et al., 2013).

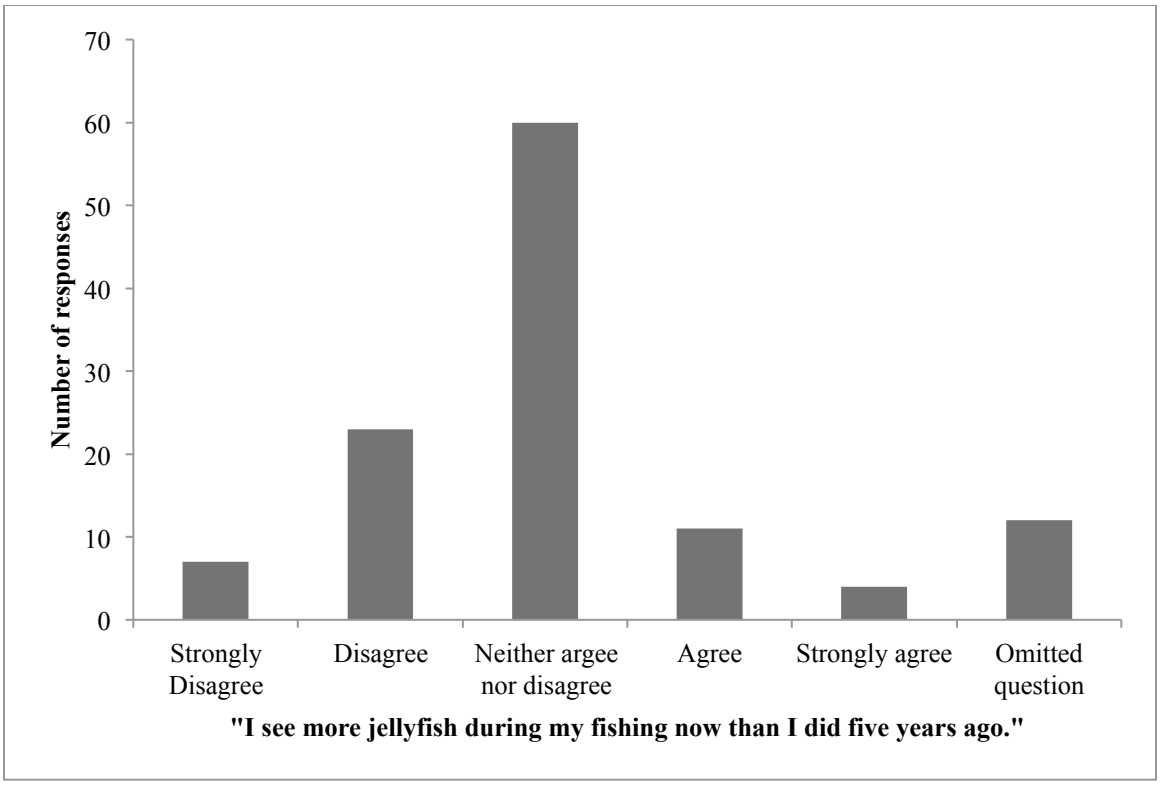

Figure 22. Fishers' responses to whether jellyfish have increased over the last 5 years (n=117).

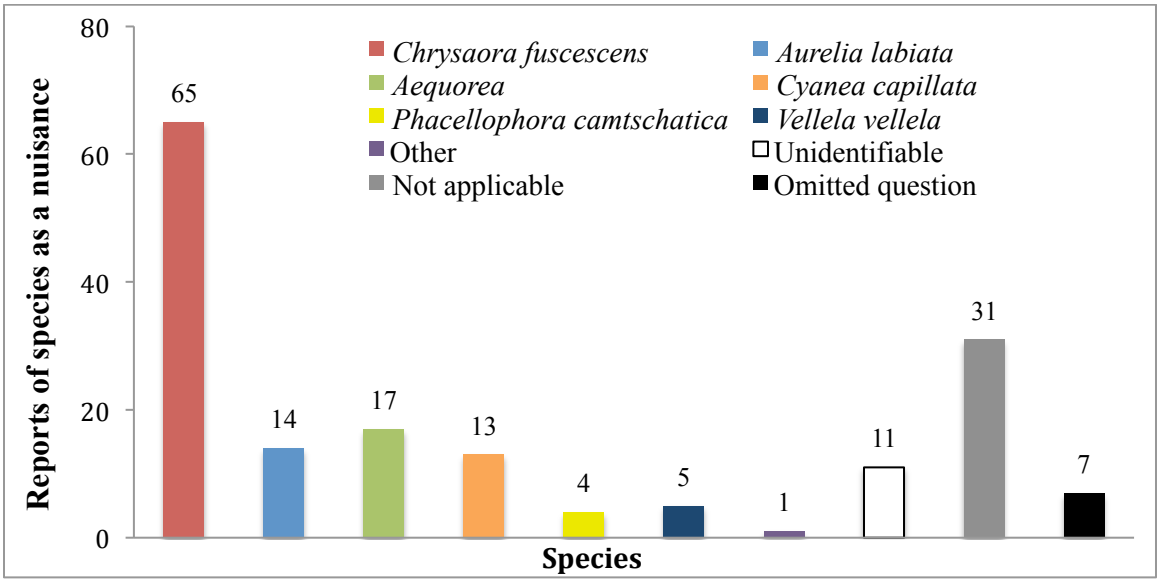

Figure 23. Proportions of species reported to account for revenue losses, identified by respondents using color photographs (n=77). If a single respondent reported multiple species, each species was counted separately. "Other" constitutes a species reported as "acorn jelly," presumably the mesopelagic coronate jellyfish *Periphylla periphylla*.

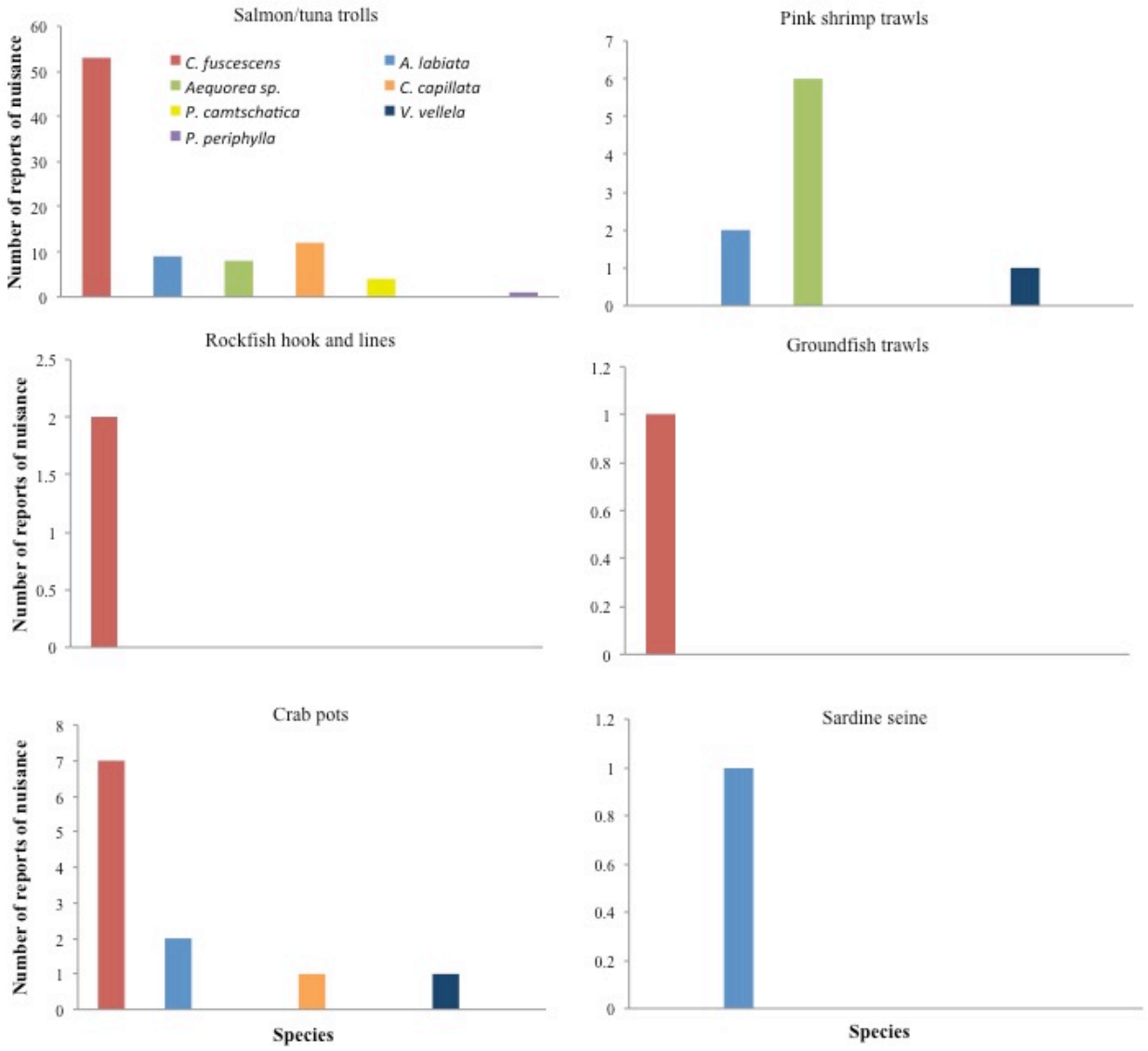

Figure 24. Proportion of scyphozoan jellyfish species reported to account for nuisance to different fishing gear types in the Northern California Current.

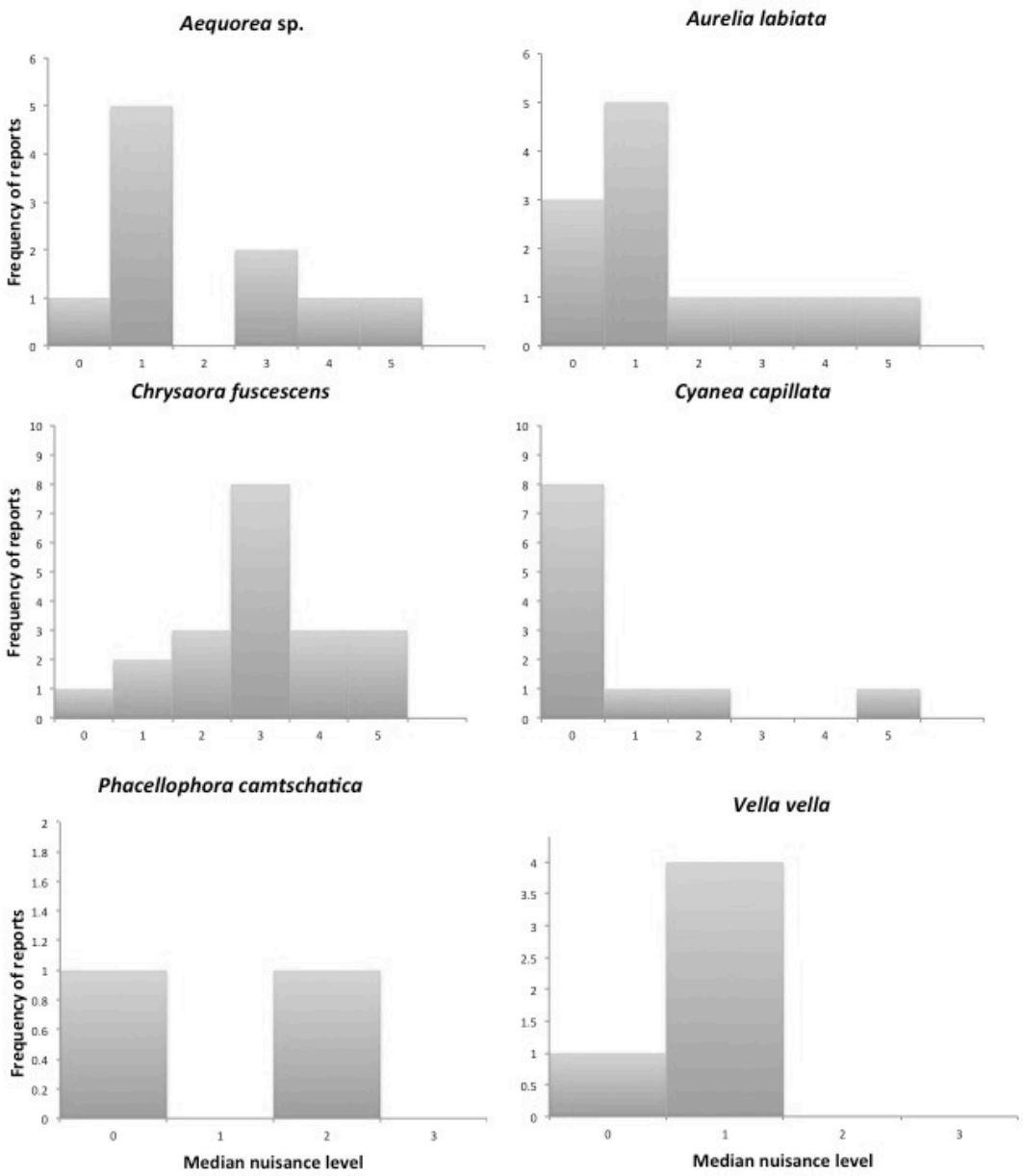

Figure 25. Histogram of jellyfish nuisance level by species. Nuisance level is ranked on a 0-5 scale with "0" corresponding to no nuisance and "5" to severe nuisance. Developed using StatPlus:mac LE.

The summaries below qualitatively detail the effects of jellyfish on different fisheries and fishing gear types. They are formulated primarily using the data provided by the 59% of respondents who reported some economic impact of jellyfish on their fishing.

Salmon and tuna trolls

Salmon and tuna trollers generally concurred that the biggest impact of jellyfish on their fishing activity was the lost time cleaning off jellyfish snared on hooks. Trollers reported that lead ball snubbers, jigs, hoochies, and flashers are the principal terminal tackles fouled. Snubbers function as shock absorbers by keeping even tension on the lures. Jigs are small metal slabs the approximate size of the baitfish on which Chinook, Coho and other Pacific salmon feed. “Hoochies” are soft, typically squid-shaped, plastic attractants, attached to hooks. Flashers are thin bright plastic or metal oblongs that create a churning motion that draw fish in from far away. These tackles attach to the end of the troll and can snag jellyfish; this requires more labor to keep the gear clean.

One respondent who has fished commercially but irregularly for 50 years reported, "It's definitely a cost because I'm always running my gear to clean off jellies. I don’t know how many fish don't bite because of jelly crap on my hooks." Additionally, when jellyfish are fouling gear, respondents reported that salmon do not bite that gear. When jellyfish snare on hooks, this necessitates that trollers pull their gear, clean off the jelly material, and reset the gear. Other trollers reported that if they encountered jellyfish while salmon trolling, they picked up their gear and relocated their fishing activity.

Jellies tended to present the greatest problem for salmon trollers who fished the shallows (inside 25 fathoms), preventing them from fishing nearshore. Salmon trollers can therefore miss out on fish that overlap with the range of bloom, particularly when blooms concentrate in channels or points (e.g. Cape Lookout, Tillamook Head).
One troller observed a notable change in the seasonal severity of impact: “No nuisance May, minimal nuisance June, minimal-moderate July, Moderate August, moderate-severe

September." Another noted, "The jellyfish have rarely been a problem above Pt. Reyes. Below there, I'd say there is considerable losses to trollers." Trollers sometimes presented contrasting opinions, alternating between acknowledgement of jellyfish as a natural part of the ecosystem—"Never really thought about lost revenue because of jellies…always accept them as part of overall experience"—and objecting to their presence—"[Jellyfish are] a major problem for fishermen at times."

Pink shrimp trawls

Pink shrimpers employ trawl boats, generally fishing between 75 and 125 fathoms (450 to 750 feet), with a mesh size no smaller than $1\frac{3}{8}$ between the knots (Oregon Department of Fish and Wildlife, 2012).

Seventy-five percent of pink shrimp trawlers reported that jellyfish do inflict revenue losses on their shrimping. As one trawler described, "When you catch jellies in your net, the water does not flow through the web, stretching the web as well as the ribline. The [net] stop[s] fishing [and fails to catch shrimp]—so you have to relocate or fix gear." All of those who indicated financial losses attributed them at least in part to the expense associated with relocating to avoid blooms.

Rockfish hook and line

The rockfish "hook and line" fishery also includes pole and line; troll; longline; cable gear, and stick gear. Rockfish fishers consistently reported that jellyfish do not affect their income or fishing activity. One respondent who fishes in Depoe Bay reported an income loss and suspected jellyfish were particularly bad there. Like salmon trollers, this respondent reported, "Some fish will not bite when [jellyfish] get on [the] hooks. Costs a couple of extra hours when I clean boat if they do not get washed off

immediately." He continued that "[Jellyfish in Depoe Bay] have always varied about the same levels for the past 40 years. Some really bad years. There's always a lot in September between 10 and 20 fathoms north of Newport in September and early October. They get concentrated in big tide rips."

Rockfish fishers and salmon trollers also often reported the impact of jellyfish on lingcod fishing, which, too, can be fished using a hook and line, or with bottom longlines, trawls, or dingle bars. Lingcod fishers reported having to stop fishing sometimes until jellyfish swarms had dissipated. Therefore, rockfish fishers and lingcod fishers may incur the cost associated with driving a boat to a reef or other fishing location where they subsequently cannot fish because of jellyfish concentrations. Additionally, jellyfish may reduce the catch rate of lingcod by fouling gear. As one respondent described, "In lingcod fishing your trolled longline 'lifts' off the bottom [and] few cod are caught as a result."

Groundfish trawls

The Pacific groundfish fishery is a mixed-stock fishery that includes 90 species of fish that dwell near the seafloor. The fishery extends 200 miles into the Pacific Ocean, along the coasts of California, Oregon, and Washington. Fishers use many different types of gear, including trawls, traps, and longlines, but trawls dominate. The trawl sector consists of two fisheries, one targeting Pacific whiting (hake) and another targeting non-whiting species. Pacific Whiting is fished almost exclusively with mid-water trawls, primarily over bottom depths of 100-500 meters (Pacific Fishery Management Council, 2011). The non-trawl sector includes fishers who use what is called "fixed gear," such as longlines and pots, and primarily targets sablefish.

Respondents from this fishery tended to report no revenue losses from jellyfish (n=4), believing that drag boats fish too far offshore (outside the 100-fathom curve) to encounter jellyfish blooms. The one respondent who did indicate financial losses from jellyfish fished south of Oregon, while the respondents who reported no losses fished in Oregon or Washington.

Crab pots

Although crabbers were not surveyed directly, some respondents commented on the impact of jellyfish on their crabbing activity. Jellyfish reportedly do not have much of a financial effect on the crabbing industry, but are sometimes caught in crab pots and get broken apart in cage mesh. As crabbers are reeling in their pots, occasionally snared tentacles get flung into their face and eyes. Crabbing crewmembers noted that such stings can be severe, still hurting days later.

Sardine seine

Since only 10 fishers hold resident ocean sardine permits in Oregon, and the survey elicited only one sardine seine respondent, this represents a 10% response rate. The respondent reported that although *Aurelia labiata* blooms did not impose revenue losses in 2012, in past years the costs of relocating to avoid blooms reduced seasonal revenue by 15%.

Discussion

This study represents the first socioeconomic survey in North America to quantify the economic impacts of jellyfish on fisheries operations. One published report exists on the direct negative effects of jellyfish on the commercial shrimping industry in the

Northern Gulf of Mexico in 2000; an impact of $10 million during a two-month concentrated "super-swarm" of invasive *Phyllorhiza puntuata* was estimated (Graham et al., 2003). This estimate, however, is based on circumstantial evidence from a transient event, whereas the impact uncovered in this study represents a calculated baseline of jellyfish interference across different fisheries. The results also represent the first report of jellyfish interference with trolling and longline gear; previous studies have found an impact only on set, trawl, and gillnets, and seines (Purcell et al., 2007). To the author's knowledge, this survey also constitutes the first published report of *Chrysaora fuscescens* reducing revenues of fishers.

Since jellyfish abundance may be indicative of ecosystem shifts (Suchman et al., 2012), establishing a "standard" socioeconomic impact across different fisheries serves as a valuable reference point. It has been suggested that the expansion of hypoxia along the Oregon shelf may favor jellyfish over fish (Brodeur et al., 2008), but according to these results, fishers have not seen this materialize, and instead suggest stable populations. If, however, changing environmental conditions in the Northern California Current were to result in jellyfish proliferation, the data from this study indicate that such a rise may have pronounced effects on already-strained fishing industries.

This survey revealed that many fishers do not equate increased labor expenditure with increased costs. Fishers may report increased hours of labor removing jellyfish snared on hooks as merely a "nuisance," whereas fuel for relocating or reduced catch because of jellyfish are considered "revenue losses." Therefore, in future studies it may prove fruitful to inquire about additional hours of labor required because of jellyfish presence, assigning an hourly rate to fishers' labor, in contrast with directly inquiring

about revenue losses. If a standardized economic value were assigned to labor, the costs associated with jellyfish blooms may be substantially higher than the values quantified in this survey.

This survey also revealed that pain caused by jellyfish stings is not a serious impediment to fishers' work. This contrasts the finding of a similar study on the nuisance of medusae to artisanal shrimp trawlers in the southern Brazilian Bight, where the cubomedusae *Chiropsalmus quadrumamus* and *Tamoya haplonema* and the hydromedusa *Olindias sambaquiensis* caused painful stings to fishers' arms and trunk, reportedly making work "extremely arduous" (Nagata et al., 2009). In this sample of fishers from the Northern California Current, crabbers were the only respondents who consistently reported that jellyfish increase the strenuousness of their work.

Respondents recalled jellyfish abundance to be the greatest in 2011. It is established within social science research, however, that people's recall is not always reliable and depends on time passed and the nature of the queried material (e.g. Bradburn et al., 1987); there may, therefore, be inaccuracies in retrospective data such as this. The "telescoping problem" in retrospective recall—wherein events the past are likely to be recalled as being more recent than they actually are—is a known and common response error, but also an inconsistent one; one cannot know for sure who has it and who does not (Bernard et al., 1984; Sudman and Bradburn, 1992). Informant inaccuracy may be reduced through the use of "good" informants, defined as people who know a lot and who can report accurately on the culture or phenomena being studied (Bernard et al., 1984). A multi-decade recall period such as the one requested in the present study may increase recall error by underestimating past jellyfish abundance, since recall could be subject to

memory loss (e.g. De Nicola and Giné, 2012). Despite this, recall surveys have been used as low-cost method for estimating fishers' catch rate and effort information (e.g. Duttweiler, 1976; Griffiths et al., 2012; Pinho et al., 2012) and through this some approximate recall parameters have been identified: periods longer than three months are generally considered too long to accurately recall catch and effort (Lyle, 1999), but rare and memorable captures, or presumably, abnormal jellyfish abundance, may be less susceptible to recall bias (Pollock et al., 1994). Respondents' recall of year(s) with maximum jellyfish abundance (Figure 21) does suggest a pattern of decadal-scale variability similar to that described by Condon et al. (2013), which indicated two periods of increased likelihood of encountering jellyfish blooms: 1971–1985 and 1993–2004.

In 2011—purportedly a year of high jellyfish abundance off the Oregon coast—there were ENSO-neutral conditions from May until July. In September, however, increased upwelling and further shoaling of the thermocline strengthened La Niña conditions across the eastern Pacific Ocean (NOAA, 2011). Different species of jellyfish appear to respond very differently to El Niño oscillations (e.g. Dawson et al., 2001; Raskoff, 2001). In the CCS, *Aurelia* and the large salp *Thetys vagina* increased in years when upwelling and offshore Ekman transport were more pronounced, while *Chrysaora fuscescens*, *Aequorea*, *Cyanea capillata*, and *Phacellophora camtschatica* increased when upwelling was weak and sea surface temperatures were elevated (Pearcy et al., 1985).

Ocean basin-wide climate oscillations are not the only factor that could account for the reported population maximum in 2011. Although this survey inquired about fishing locations on a meso-scale since fishers can be reticent to share their fine-scale

fishing locations, some respondents volunteered specific fishing locations that consistently experience problematic jellyfish abundance, as well as the locations that tend to be jellyfish-free. The predictability of jellyfish aggregations around physical promontories including Point Reyes Peninsula, Tillamook Head, and Cape Lookout, suggests that physical factors may be partly responsible for the location and extent of patches of medusae. Cape Blanco—the largest offshore extension on the West Coast—was not reported to be a nuisance area for jellyfish, although *Aurelia labiata* concentrations are known to occur directly south of this region (Suchman and Brodeur, 2005) and mass occurrences of *Aurelia* has caused nuisance to fishers in other parts of the world (e.g. Baumann and Schernewski, 2012). Fishers' accounts of increased gelatinous zooplankton biomass in shallow sites is consistent with existing literature, and may be explained by the increased primary productivity in estuarine and neritic zones (e.g. Lilley et al., 2011).

The limitation of a survey structured in a manner such as this one is that it may be subject to volunteer bias—those fishers who have experienced the most severe nuisance from jellyfish may be the most eager to participate in surveying, whereas those who have felt no impact do not feel inclined to participate—or response bias—where respondents answer questions in the way they think is socially desirable or what the questioner wants to hear. However, the results in this study showed fishers readily selected neutral answers such as "neither agree nor disagree," occasionally wrote in their own answers when a suitable answer was not available, and reported "unknown" rather than providing an inaccurate estimate of revenue losses. This suggests that fishers may be impervious to these potential biases, perhaps because the commercial fishing industry is structured

within a cultural model characterized by independence in behavior and thinking (Martin, 2006; Thomas et al., 1995; Valdés-Pizzini, 1990; Van Ginkel, 1996).

This study documents the value of fishers as collaborators in scientific research, particularly for documenting population trends. Although a growing body of literature indicates indicated that fishermen's local ecological knowledge (LEK) may have the potential to improve fishery management (e.g. Silvano and Valbo-Jørgensen, 2008), this knowledge may prove even more useful for poorly-studied organisms such as scyphozoans, for which long-term time series of abundance are often lacking. As one fisher said, "I have observed for a long time."

CHAPTER V

SOCIOECONOMIC IMPACTS OF JELLYFISH ON CALIFORNIA HALIBUT DRAGGERS

Introduction

The California Halibut (*Paralichthys californicus*) bottom trawl fishery was analyzed separately from other survey data because the fishery has substantially fewer active permit-holders (n=25) and the fishing grounds are in a separate region, predominantly off the California coast. The halibut fishery also has much lower physical landings than other fisheries, with higher-price catch intended for a high-end live market (CDFG, 2008).

P. californicus is a slow-growing pleuronectiform (flatfish), maturing after two or three years (Fodrie and Levin, 2008). An estuarine-inner shelf species, its distribution is centered in the coastal waters of northern B aja California, while the fishery is concentrated from Bodega Bay in northern California to San Diego in southern California (Ish and Stroman, 2006; Moser and Watson, 1990). As *P. californicus* grows it moves from nursery grounds in bays to sandy benthos along the open coast, typically at depths less than 60 meters (Allen, 1990).

The first landing records of commercial halibut date back to the mid 1910s, and landings peaked in 1919 (Wertz et al., 2004). The fishery has historically suffered from overfishing and other forms of anthropogenic impact, including pollution of and development in the environs of estuarine nursery habitat (Allen and Herbinson, 1990). While landings declined precipitously from 1920 to 1930, and again from 1950 to 1960,

landings rebounded slightly after 1970 and have remained relatively constant since 1995 (Wertz et al., 2004). The California halibut fishery operates year-round in southern California, but is most active during the winter and spring (Barsky, 1990). The fishery is split into two stocks—a central and a southern—separated at Point Conception. In the central fishery, most of the catch is taken during the summer (Herrick and Hanan, 1988). *P. californicus* is a species of great economic importance to the southern California region, despite the relatively small number of active permit-holders. Many fishing villages in Baja owe their livelihoods to the commercial importance of halibut, particularly the village of La Bocana in Baja California Sur, whose fisher-owned co-op processes a daily average of 600 halibut when in season (Bruns 2012).

The California Department of Fish and Game completed its first-ever stock assessment for California halibut in 2011, concluding that the central population is well above the biomass associated with maximum sustainable yield, increasing substantially since 1980 due to high recruitment, while the southern population is depleted to about 14% of its unexploited spawning biomass level.

Management of California halibut has long been a state prerogative. New regulations required by the California Senate Bill (SB) 1459 have closed portions of the traditional halibut trawl grounds. In 2006, a restricted access program, the California Halibut Bottom Trawl Vessel Permit program, went into effect, which created a state-issued California halibut bottom trawl permit and prohibited trawling in designated California Halibut Trawl Grounds without this permit (CDFG, 2008). To qualify for a permit, landing records of a minimum of 200 pounds in at least two of the calendar years from 1995 to 2003, or one of the calendar years from January 1, 2004, to February 19,

2004 are required. Prior to the introduction of the vessel permit program, halibut dragging was regulated under California Fish and Game Code Section §8836 (effectively repealed by SB No. 1459), which permitted trawling for multiple bottomfish species in waters three or more nautical-miles from the mainland shores of Districts 17,[2] 18,[3] and 118.5,[4] including portions of Monterey Bay, Estero Bay, and San Luis Obispo Bay. Perhaps the largest consequence of the passage of SB 1459 was to prohibit trawling in the portions of Monterey Bay that were formerly fishable. A state-permit is now required in state waters 0-3 nautical miles from shore, whereas a federal groundfish trawl permit is necessary in federal waters, the Fishery Conservation Zone (3-200 nautical miles) (SB No. 1459, 2004).

The restricted access program has resulted in a decrease in landings from a peak of 596 tons in 1999 to a low of 174 tons in 2007 (Sweetnam, 2008). Annual ex-vessel revenue has witnessed parallel declines during this same time period, ranging from a high of $3.3 million in 1997 to a low of $1.8 million in 2007 (Sweetnam, 2008). Annual catch has been highly variable, and though the root cause of this instability remains slightly

[2] includes the waters and tidelands to high-water mark of Monterey Bay and the Pacific Ocean, lying between a line extending west from Pigeon Point Lighthouse and a line extending west from Yankee Point, Carmel Highlands in Monterey County, excluding the areas included in District 16, and excluding all rivers, creeks, sloughs and lagoons emptying into the Pacific Ocean and Monterey Bay within the boundaries thus defined.

[3] includes the ocean waters of the state and tidelands to high water mark from Yankee Point of a line extending from the south boundary of Santa Barbara County westerly through Richardson Rock excluding all rivers, streams and lagoons.

[4] includes ocean waters and tidelands not included in other districts, bounded by a line beginning at the intersection of the common boundary of Monterey and San Luis Obispo counties, thence due west two miles to a point, thence southerly and parallel to the coastline two miles south of the common boundary of Santa Barbara.

unclear, it may be attributable to loss of shallow water nursery habitat to dredging and the development of bays (California Department of Fish and Game, 2003).

Within the directed California halibut trawl fishery, there are currently 48 permitted vessels. Based on 2012 fishing activity, 25 of these permit-holders are active participants with homeports from San Francisco to Los Angeles (T. Tanaka, California Department of Fish & Game, personal communication, November 20, 2012). California halibut fishers can employ three gear types: hook-and-line, trawl, and set gill net. This survey assessed "light touch" trawl gear—the most productive of the halibut-targeting gears and the largest contributor to total commercial landings (Sweetnam, 2008). For halibut trawls, the California Department of Fish and Game requires a minimum codend mesh size of 7.5 inches and the webbing of the entire trawl net must not exceed 7 millimeters in diameter.

The bycatch rate for halibut draggers is approximately 56 pounds/hr. The most recent study, conducted in 2007, calculated that the most commonly caught bycatch consisted of 0.74 pounds of crabs, 0.71 pounds of bat ray, 0.39 pounds of sharks, and 0.16 pounds of skates per-pound of California halibut (CDFG 2008). Trawl nets may also capture large numbers of unwanted jellyfish, which, at 95% water, can be heavy to tow and retrieve (Honda et al., 2005; Uye, 2005). This unintended entrapment of jellyfish may damage nets and captured fish, or exclude desired fish (Park et al., 2011). In addition to the direct effect on trawl gear and target species, presence of jellyfish in the codend of a trawl may also increase mortality of discarded bycatch (Broadhurst et al., 2008)—an effect that may be particularly consequential in a fishery that depends on a live market. Anecdotal evidence from fishers at Fisherman's Wharf in San Francisco, CA suggested

that halibut draggers are among those most severely affected by jellyfish in the CCS. In an effort to quantify these impacts, a mail survey of active permit-holders was conducted to determine the magnitude of economic damages caused by jellyfish.

Methods

On December 4th, surveys were mailed to active California Halibut trawlers (n=25) with assistance from the California Department of Fish and Game in Monterey, CA. Fishers were asked to estimate the indirect damages caused by jellyfish—including costs of relocating to avoid blooms, lost fishing time, lost time to bycatch sorting, fish depreciation, or gear damage. In an attempt to account for differences in average revenue between vessels, cost estimates were requested both as a numerical value and as a percentage of seasonal revenue. The frequency and severity of jellyfish stings was concurrently evaluated. Fishers were also asked to assess whether or not they had observed a noticeable change in jellyfish populations over the past five years. Draggers were asked to identify jellyfish to species-level, using color photographs for reference (Figure 28). Sample photographs of three common salps in the Northern California Current were provided in the survey alongside photographs of scyphozoans, but due to the morphological similarity between salp species, these responses were aggregated within the class Thaliacea, which includes salps, pyrosomes and doliolids.

Results

Four California halibut draggers returned surveys, which corresponds to a 16% response rate. Respondents represented the central and southern coast—from Point Arena to the Mexico border. All respondents reported that jellyfish reduce their seasonal revenue. Although all respondents were active halibut draggers, two respondents listed

"salmon trolls" as the gear type most disrupted by jellyfish. Respondents reported fishing at depths ranging from 5-60 fathoms. The ways jellyfish reportedly affect these fisheries include: fishing activity must be relocated, fishing time must be shortened, jellyfish fouled fishing gear, and jellyfish bycatch increased sorting time of catch. The "nuisance level" associated with this impact ranged from moderate to severe, with a median of moderate-severe (level 4 out of a 5-point ranking scale). Revenue losses ranged from $2,000-$30,000—representing 1% to 50% of seasonal revenue in years with high jellyfish abundance. To account for these revenue losses various species were identified, but thaliaceans were predominantly reported to cause impacts rather than scyphozoans (Figure 26). All respondents reported that the revenue losses incurred this season were more than in past seasons, and all respondents agreed (n=3) or strongly agreed (n=1) that jellyfish populations appeared to be increasing in their respective trawling grounds.

Two particularly informative descriptions of the jellyfish conditions in California are provided below:

1. [*I*] [*h*]*ave to tow trawl after each short tow as it is so heavy with jelly it won't fish. Half day is lost because of this. Salmon trolling gear must be run steady as salps are on all hooks and flashers-snaps. In the Santa Barbara you could not find a clear area. This is the third year this has happened. Third year of cold water. In our area the purple stripe* [Chrysaora colorata] *is common. These were not around. No baitfish or larger fish are around in this poison water, which makes it very hard to make a living.*

2. *When heavy jellyfish show up I can't avoid them by moving location anymore while fishing halibut. In the 1950s, 60s, 70s, 80s, we would move offshore for Petrale* [sole]*, English* [sole]*, Rock Cod, or Dover Sole, but since the government* [Pacific Coast Groundfish] *buy back program I don't have deep-water permits and just target California Halibut with incidental bycatch to supplement my fishing income. Jellyfish* [were] *more of a problem when all the trawls were cotton twine. Synthetics such as nylon, poly, etc. are stronger and cut jellyfish more. Jellyfish often show*

up at other times of the year [besides June through September] *in our area.*

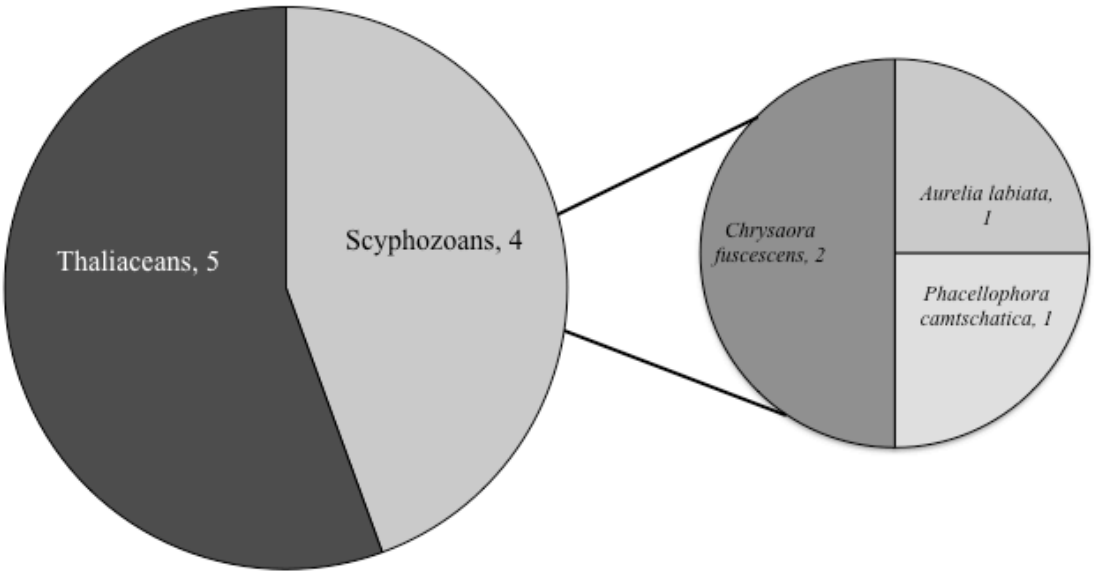

Figure 26. Species responsible for causing revenue losses to California halibut trawlers fishing from Point Arena to the Mexico border. The number followed by the species name indicates that number of respondents who identified that particular species as a nuisance. There were nine responses obtained from four respondents in a multiple response question (i.e., each fisher could check more than one species responsible for nuisance).

Discussion

Although this survey of California halibut draggers is a small sample, the responses suggest markedly different abundance trends for gelatinous macrozooplankton than the general survey of fishers in the CCS contained in this same thesis. Revenue losses are dominated by pelagic tunicates rather than Cnidarian scyphozoans. The financial losses documented by California draggers tended to be of greater magnitude than reported by fishers whose activity is concentrated north of Point Arena.

This survey also uncovered one important way that fisheries management—namely, that a federal groundfish permit *and* a state halibut permit are now necessary if one is fishing within and beyond three miles from shore. The requirement of state-issued

licenses to participate in the California halibut fishery in state waters (introduced by SB 1459 in 2006) has restricted trawlers' ability to move offshore to avoid jellyfish because, generally, halibut vessels operating in state waters do not hold a federal limited entry groundfish trawl permit (CDFG 2008). The impact of this program has, according to one respondent, reduced fishers' ability to relocate to avoid jellyfish blooms, which, to the author's knowledge, is the first account of its kind.

Literature documenting the disruption of salps on fishing activity is much scarcer than that for jellyfish. The references for salp aggregations potentially influencing human activities are almost exclusively for the Southern Ocean, where salps (mainly *Salpa thompsoni*) are suspected to be increasing at the expense of Antarctic krill (*Euphausia superba*) and thereby may indirectly have negative effects on the upper trophic levels, including commercially-harvested fish (Atkinson et al., 2004; Loeb et al., 1997; Pagès, 1997). A few exceptions are worth noting. A marked decline of the herring fishery in the northern part of the North Sea in 1921 coincided with the occurrence of large quantities of salps, and published communications between scientists at the time suggested the possibility of connection between the two (Lucas and Henderson, 1936; McIntosh, 1925). Although McIntosh (1925) disproved this hypothesis by observing that the herrings consume the salps, he does note that "if the tow-nets and collecting vessels are not quickly attended to, the small jelly-fishes and ctenophores (*Thaumantias* and *Pleurobrachia*) levy a heavy toll on the young fishes" (p. 911). An unusually extensive invasion of *Salpa fusiformis* in May and November 1955 off the coast of Norway was described as "a serious drawback to the fisheries" (Brattström, 1972). More recently, a sudden abundance of salps off the coast of Washington resulted in some salps snaring in

commercial and recreational crab pots; while these were purportedly of no nuisance, one article concluded that "if the population increases, commercial crabbers and others are concerned the creatures could affect the local economy and environment" (Chittim, 2013).

Salps feed primary on phytoplankton and marine microbes (e.g. Harbison and Campenot, 1979; Vargas and Madin, 2004). Unlike scyphozoans, then, salps tend not to be direct trophic competitors with fish, although indirect ecological interactions may still exist (Purcell and Arai, 2001). By decreasing the microbial populations that support the crustacean zooplankton populations, for example, salp blooms may reduce food supply for nekton (Boero et al., 2008) Alternatively, many species of fish, including sablefish (*Anoplopoma fimbria*) and butterfish (*Peprilus*) have been documented to feed on pelagic salps (Arai et al., 2003), so the recent reported abundance may not be entirely negative for all fisheries. Additionally, unlike scyphozoans, salps lack stinging nematocysts, and therefore do not threaten to reduce the commercial value of captured fish through stinging. Nor do they pose the same health and safety risks to fishery laborers.

In the California Current region, thaliaceans are common in upper layers of warm, offshore waters with high phytoplankton biomass, and are only occasionally dominant in coastal upwelling areas (Blackburn, 1979). The most abundant species of thaliacians in the CCS are *Dolioletta gegenbauri* (Thaliacea: Doliolidae), *Doliolum denticulatum* (Thaliacea: Doliolidae), *Thalia democratica* (Thaliacea: Salpidae) and *Salpa fusiformis* (Thaliacea: Salpidae) (Blackburn, 1979; Lavaniegos and Ohman, 2003). *Dolioletta gegenbauri,* a small, coolwater doliolid, represents the largest contributor to mean carbon biomass in Southern California Bight, but is most abundant north of San Francisco

(Lavaniegos and Ohman, 2003); our respondents primarily fished below this range and therefore *D. gegenbauri* is unlikely to constitute as much of a disruption to this fishery. Additionally, because doliolids are small and extremely fragile, they are likely to pass though nets whereas most salps, with their thicker tunics, would be more likely to clog in nets and prevent gear from fishing properly. A cosmopolitan species, *Salpa fusiformis* is one of the most abundant salps in the CCS in springtime, known to form massive blooms that have been documented to reach 492mg C m^{-2} in the CCS and elsewhere (Harbison and Campenot, 1979; Lavaniegos and Ohman, 2003; Madin et al., 2006). Unlike *Chyrsaora fuscescens*, high densities of *S. fusiformis* tend to be concentrated off the continental shelf break in oligotrophic waters dominated by small phytoplankton (Laval et al., 1992).

The overall trend of Cnidarian and Thaliacian populations off the California coast is uncertain. Analysis of mean biomass (log_{10} mgC m^{-2}) of pelagic tunicates sampled from CalCOFI stations from 1950 to 2002 show significant declines (Lavaniegos and Ohman, 2003); however, this analysis includes pyrosomes, doliolids, appendicularians, and salps and therefore may not be representative of salp trends exclusively. A separate analysis of jellyfish (Cnidaria, Ctenophora, and Chordata) population trends in the California Current System after 1950 using fuzzy logic analysis found that populations were increasing, but with a low "conclusion certainty" score (Brotz et al., 2012). This latter analysis relied on both anecdotal information and scientific, peer-reviewed literature, including the same CalCOFI data from Southern and Central California sampling stations analyzed by Lavaniegos and Ohman (2003), but also incorporating references to jellyfish abundance trends from Prince William Sound, Washington, Coos

Bay, Oregon, and Baja, Mission Bay, San Diego Bay, and San Francisco Bay, California (Brotz, 2011). Amidst this context of scientific uncertainty, many fishers are among the most acute observers of the marine environment; therefore, the population increases reported by respondents in this study merit consideration. Additionally, the present permit system for the California halibut fishery went into effect in 2006 and required landings between 1995 and 2003 to qualify for permits; its present permit-holders are therefore primarily fishers with extensive experience (Travis Tanaka, California Department of Fish and Game, personal communication, 15 April, 2013). One respondent, for example, was 91-years old and had fished for seventy years. Presumably, these and other long-term fishers have improved their ability to reduce jellyfish bycatch and other nuisances over time (e.g. Brotz, 2012; Kendall, 1990; Matsushita & Honda, 2006). Artisanal shrimpers in the Brazilian Bight, for example, have been documented to modify their nets, reducing the vertical opening of the trawl, to help prevent medusae from entering and clogging the cod-end (Nagata et al., 2009). Accordingly, the reported increase is presumed to reflect an increase in the amount of jellyfish present rather than an increase in encounter rate.

Experimentation with jellyfish exclusion devices is underway in Korea, China, and Japan (Matsushita et al., 2006; Park et al., 2011; Peng et al., 2007). Turtle exclusion devices (TEDs) employed in Australia's northern prawn fishery have been modified to simultaneously reduce jellyfish bycatch and increase prawn catch (Cox et al., 2007). Soft-type TEDs, which consist of exclusion nets without metal frames, have successfully excluded the cannonball jellyfish (*Stomolophus meleagris*) from shrimp trawls in the southeastern U.S. (Kendall, 1990). A Jellyfish Excluder Device (JED) has been invented

for towed fishing gear to reduce bycatch of *Nemoplima nemurai* in Japan (Matsushita et al., 2006). Such developments hold promise for reducing the impact of jellyfish on fishers. Other proposed management measures include using cutting nets to destroy jellyfish in the water column and the use of biocontrol agents on benthic polyps (Richardson et al., 2009), but these have the potential for cascading environmental consequences. Bycatch reduction devices are, in comparison, a low-risk way of managing the negative effects jellyfish may impose on fisheries.

While the four responses received in this survey may be insufficient to draw firm conclusions about the comparative effects of salps and jellyfish on California draggers, they offer a useful starting point from which more in-depth analyses may be initiated. The results presented here offer strong evidence that salp abundance, in addition to jellyfish abundance, can levy significant impacts on nearshore trawl and troll fishing.

CHAPTER VI

GENERAL CONCLUSIONS

Broadly, the goal of this study was to better understand scyphozoans in the Northern California Current at different life stages, and to examine the interface between scyphozoans and anthropogenic activity—primarily coastal development and commercial fishing. This thesis has identified the nature and respective magnitudes of jellyfish interference with multiple fisheries within the CCS, the species responsible for this interference, and the severity of nuisance associated with fishing locations across the Pacific Region. The study also sought to determine whether *Chrysaora fuscescens* planulae exhibit substrate selection behavior. The literature on planulae settlement and pre-metamorphic behavior is relatively sparse, but from the few studies that have been conducted it can be concluded that different species of scyphozoans exhibit markedly different larval settlement preferences. It is probable that these behaviors have direct ecological consequences, but future work must connect quantitative laboratory settlement preference data with observed spatial patterns of recruitment in the field. The study also sought to answer whether the scyphistomae under the Charleston Marina docks, which previously had never been identified to species-level, were *C. fuscescens*.

The results of this analysis show that jellyfish and salps, even in ordinary abundance, increase the cost of fishing effort for multiple fisheries within the Northern California Current. Trolls were the gear type respondents most frequently reported to be influenced by jellyfish—a gear previously assumed to insulated from the negative effect of jellyfish in comparison to trawls, set-nets, or seines. Since most of the socioeconomic impact studies for jellyfish are conducted in response to anomalous abundance or a

sudden invasion, this study contributes a novel account of the "routine" impact of jellyfish—a crucial baseline for a class of organisms whose annual abundance can vary dramatically.

This study identified a previously undescribed colony of *Aurelia labiata* scyphistomae—only the second to be located on the Oregon coast. Since these scyphistomae are conveniently established on the undersides of multiple docks directly across the street from the Oregon Institute of Marine Biology, future opportunities are rife for documenting the ecology of these scyphistomae—including when they strobilate, which no one to date has observed. Although I did not attempt to locate the scyphistomae of *Chrysaora fuscescens*, the results on the settlement preferences of the planulae can help dictate where future field surveys are conducted.

Despite the abundance of *Chrysaora fuscescens*, it has received comparatively little attention from the scientific community. Aside from one laboratory study detailing its life history, all research has focused on the medusa phase. This study has documented the profound effects of medusae fishing activities, but future research should be devoted to all stages of the life history. This thesis contributes the first experimental study of *C. fuscescens* planulae, but this experiment is of limited value without comparative field observations of settlement.

Since *C. fuscescens* is known only as an adult, we presently cannot accurately interpret its population dynamics and distributions. In this respect, *Chrysaora* is emblematic of a larger unknown about, or disconnect between, planktonic and benthic life stages: our incomplete knowledge of the life histories of most scyphozoans is a

central obstacle to understanding, and ultimately predicting, bloom events. Completing these life histories is therefore an area that should be prioritized for increased research.

APPENDIX

SURVEY IMAGES

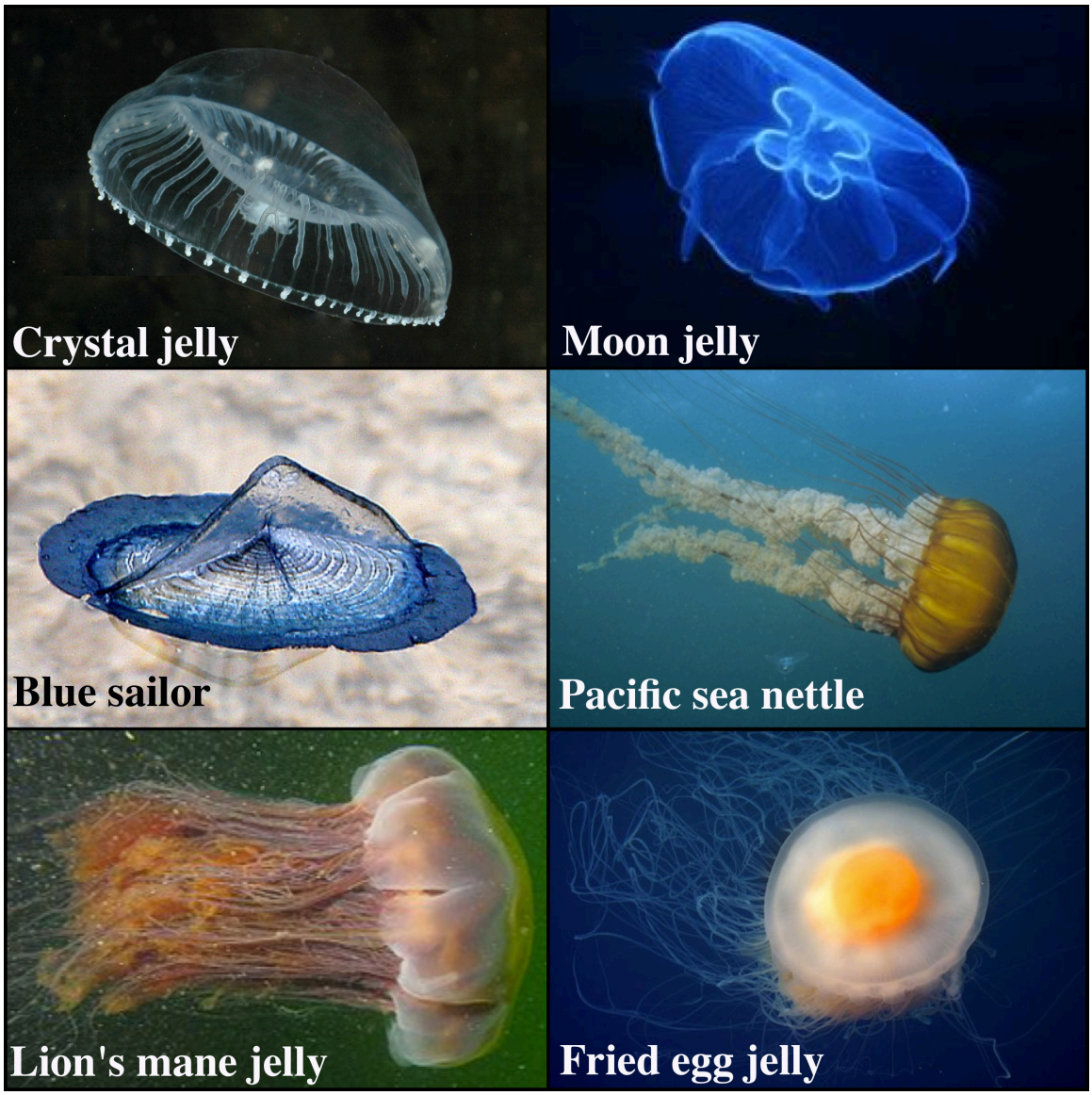

Figure 27. Photographs similar to those provided to resident permit-holding commercial shrimpers, salmon trollers, and rockfish (black, blue) and groundfish limited-entry permit holders in mailed survey, used to identify jellyfish to species-level. Photo credits: *Aequoea*: Sierra Blakely; *Aurelia*: Ecomare: *Vellela*: Proteccioncivil.org; *Chrysaora*: Monterey Bay Aquarium; *Cyanea*: Dan Hershman; *Phacellophora*: http://life-sea.blogspot.com.

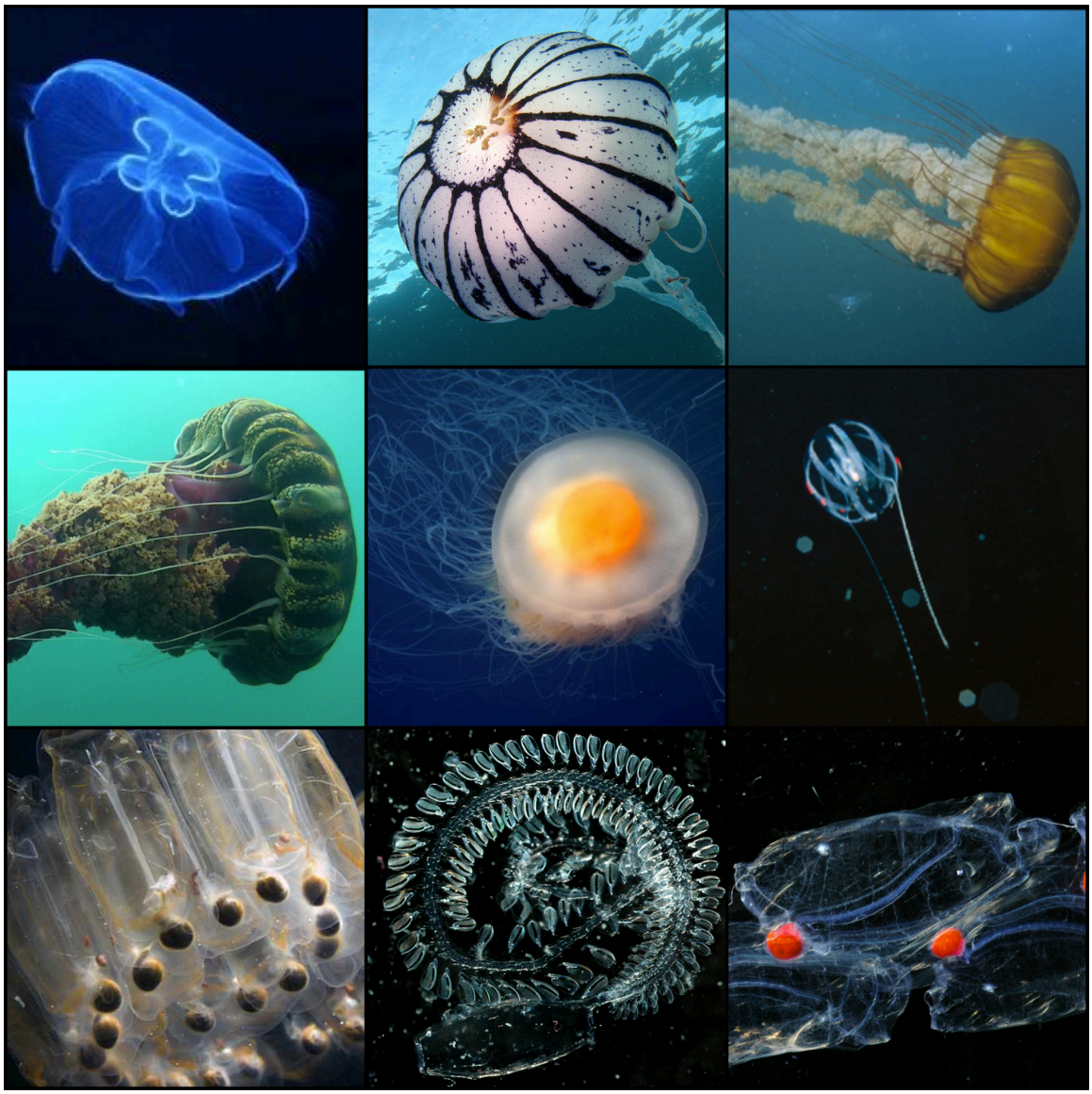

Figure 28. Photographs similar to those provided to active permit holding California halibut draggers in mailed survey, used to identify jellyfish to class-level. Photo credits: *Aurelia*: Ecomare: *Chrysaora colorata*: lemurdillo; *Chrysaora fuscescens*: ; *Chrysaora achlyos*: Michael Bear; *Pleurobrachia*: Norbert Wu/Minden Pictures; *Phacellophora*: http://life-sea.blogspot.com; *Thalia*: Gavin Newman / Greenpeace; *Dolioletta*: Larry Madin, Woods Hole Oceanographic Institution; *Salpa*: Russ Hopcroft, University of Alaska-Fairbanks.

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