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Contributions of forage fish species to marine ecosystems and anthropogenic threats to

their conservation

A Dissertation Presented

by

Konstantine John Rountos

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Doctor of Philosophy

in

Marine and Atmospheric Science

Stony Brook University

May 2014

Stony Brook University

The Graduate School

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Abstract of the Dissertation

Contributions of forage fish species to marine ecosystems and anthropogenic threats to

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2014

Forage fish are small pelagic species (e.g. sardine, anchovy, krill, etc.) that are generally short-lived and exhibit schooling or shoaling behavior. Although these species were once thought to be inexhaustible, they are prone to collapses due to oceanographic factors and overexploitation from fisheries. In addition, the effects of climate change, habitat destruction, pollutants, and harmful algal blooms threaten their conservation. Prior to the work described in this dissertation, no global assessment of the ecological and economic importance of these species had been conducted, despite the fact that these species represent some of the largest fisheries in the world and are prey for many marine predators, including seabirds, marine mammals, and large predatory fish. This dissertation explored the global importance of forage fish species to marine ecosystems and fisheries and elucidated the threats posed from the geographically expanding ichthyotoxic dinoflagellate, *Cochlodinium polykrikoides*. Using a synthesis of ecosystem models (Ecopath), forage fish were found to contribute a total of $16.9 billion USD to global fisheries value annually. While the global catch value of forage fisheries was $5.6 billion, fisheries supported by forage fish were more than twice as valuable ($11.3 billion). Forage fish also made significant contributions to marine predators, accounting for large fractions of the diets of seabirds, marine mammals and large predatory fish. For example, the median forage fish diet of seabirds in upwelling ecosystems was estimated at 89%. Other indices computed revealed that these predators: 1) often selected forage fish as their most preferred prey item, 2) commonly exhibited specialized feeding strategies, and 3) targeted similar trophic levels of prey as forage fisheries. Toxicity experiments conducted with *C. polykrikoides*, using three forage species common to the US East Coast, revealed: 1) significant mortalities occurred in both exposed embryos and eleutheroembryos, but that sensitivity differed among fish species and life stages, 2) the first evidence of sublethal impacts to fish, as exposed eleutheroembryos lost and regained their swimming ability following short-term exposures, and 3) the first assessment of behavioral toxicity in larvae following sublethal exposures. Future research should clarify these roles and continue to examine threats to forage fish populations.

Dedication Page

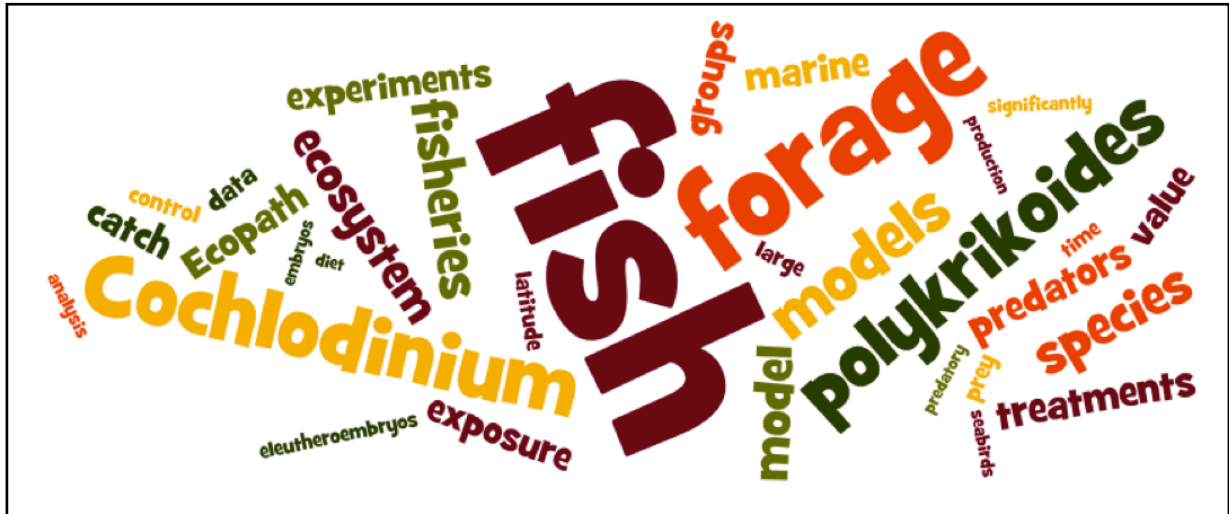*To my wife, family and friends for their constant love, encouragement, and humor.*

To my loved ones long passed, I know you will be smiling.

You all made this work possible.

Love,

Konstantine

Frontispiece

"Word cloud" of the most common terms in this dissertation.

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Chapter 1. General introduction

1.1 The state of coastal marine ecosystems and fisheries

Humans have associated with and benefited from coastal marine ecosystems, including estuaries and bays, for hundreds of thousands of years (Erlandson & Rick 2008). These ecosystems are arguably some of the most valuable on Earth, supporting both a wide diversity of marine life and essential ecosystem services (Costanza et al. 1997, Barbier et al. 2011). Coastal ecosystems, defined as extending 200 nautical miles from the shoreline, are particularly important to fisheries, as the majority of the global marine catch derived from these productive areas (Watson et al. 2004, FAO 2010, 2012). This is not surprising, as coastal ecosystems serve important roles for various life-stages of many commercially important species. For example, many larval and juvenile fish and shellfish benefit from important nursery habitats (e.g. seagrasses, mangroves etc.) found in these ecosystems, while adult conspecifics benefit from the productive foraging areas provided (Kikuchi 1980).

Many coastal marine ecosystems are becoming increasingly degraded as a result of a combination of both natural and anthropogenic influences. Negative effects of a variety of anthropogenic influences are now evident in these ecosystems worldwide (Lotze et al. 2006, Halpern et al. 2008, Rabalais et al. 2009). Coastal ecosystems are becoming increasingly eutrophic (Cloern 2001, Rabalais et al. 2009), facing the expansion and persistence of harmful algal blooms (Anderson 2009, Kudela & Gobler 2012) and experiencing rapid losses of important nursery habitats (Lotze et al. 2006, Waycott et al. 2009). In addition, marine ecosystems are experiencing declines in biodiversity and collapses of many fisheries (Jackson et al. 2001, Mullon et al. 2005, Worm et al. 2006). Understanding the ecological and economic consequences of these and other impacts individually and synergistically remains a major challenge for scientists and managers (Halpern et al. 2008).

1.2 Importance of forage fish in marine ecosystems

"Forage fish" are small to medium-sized pelagic species (e.g. silversides, sardines, anchovies, herrings, krill, etc.) of great ecological importance to marine ecosystems (Pikitch et

al. 2012). These species occupy central positions in marine food webs. They consume plankton and are preyed upon by higher trophic level predators. In this role, forage fish transfer energy up marine food webs (Cury et al. 2000, Cury et al. 2003, Fréon et al. 2005, Bakun et al. 2010) to a variety of consumers including commercially important fishes (Pikitch et al. 2012). Forage fish species naturally fluctuate in abundance in accordance with seasonal, annual, and inter-decadal variations in oceanographic forces (Barber & Chavez 1983, Francis et al. 1998, Polovina et al. 2001, Chavez et al. 2003). These fluctuations can have large impacts on marine predators, especially those with diets dominated by forage fish (Pikitch et al. 2012). Many of these predators, including marine mammals (Thompson et al. 1996, Pauly et al. 1998b, Weise & Harvey 2008), seabirds (Crawford & Dyer 1995, Jahncke et al. 2004, Furness 2007, Daunt et al. 2008), and larger fish (Walter & Austin 2003, Butler et al. 2010, Logan et al. 2011, Magnussen 2011) may be particularly vulnerable to declines in forage fish biomass (Cury et al. 2011, Smith et al. 2011, Pikitch et al. 2012). When natural fluctuations in forage fish abundance are overlaid with anthropogenic impacts, such as extractive fisheries and or diminishing water quality, the effects on forage fish populations can be substantial (FAO 2010, 2012, Pikitch et al. 2012). These factors acting together, or in any combination, can lead to negative impacts to predator reproduction (Sunada et al. 1981, Becker & Beissinger 2006), breeding (Crawford & Dyer 1995, Cury et al. 2011) and abundance (Crawford & Jahncke 1999, DeLong & Melin 2000, Jahncke et al. 2004). Such ecological impacts can have large and often unquantifiable economic effects, as many forage fish predators are aesthetically (e.g. the global whale watching industry is 2.5 billion USD annually (Cisneros-Montemayor et al. 2010)) or commercially valuable (e.g. fisheries for tuna, cod etc. (FAO 2012)).

Modern industrial fisheries have exploited forage fish species since the early 1950s (Alder et al. 2008). Currently, forage fisheries are some of the largest commercial fisheries in the world in terms of catch, with the Peruvian anchoveta (*Engraulis ringens*) purse-seine fishery topping this list (FAO 2010, 2012). Forage fisheries now occur across broad latitudes from the tropics to the Earth's poles and represent a large and growing fraction of the world's marine catch (Alder et al. 2008, FAO 2010, 2012).

Nearly 90% of the forage fish catch is used by reduction industries which produce fishmeal

and fish oil products (Alder et al. 2008). Reduction industries sell their forage fish products for the production of pet, livestock, and fish farming feeds (Alder et al. 2008, Naylor et al. 2009). As demand for these products is not expected to wane, there is growing concern for these exploited fish (Naylor et al. 2009, Tacon & Metian 2009, FAO 2010, 2012). In terms of value, forage fisheries contribute $5.6 billion (2006 USD) annually, or approximately 7% of the total global marine commercial catch value (Sumaila et al. 2007). The vast majority (>90%) of this forage fish catch is derived from coastal marine ecosystems (Watson et al. 2004, FAO 2010, 2012).

1.3 The growing threat of harmful algal blooms to coastal ecosystems and fisheries

Harmful algal blooms (HABs) have increased in geographic extent, frequency, and duration in many coastal areas worldwide (Hallegraeff 1993, Anderson 2009, Kudela & Gobler 2012). Many of these HABs produce biotoxins (Hallegraeff 1993, Landsberg 2002) that have been implicated as the cause of mass mortalities in both wild and farmed fish and shellfish species globally (Shumway 1990, Whyte et al. 2001, Lee et al. 2002, Imai et al. 2006, Anton et al. 2008, Gobler et al. 2008, Richlen et al. 2010). While these observed mortalities are significant, the impacts of HABs in altering ecosystem dynamics are far less evident (Smayda 1991, Kudela & Gobler 2012). For example, we are only beginning to understand the potential ability for HAB toxins to transfer through marine food webs and the consequences of such transfers (Geraci et al. 1989, Smayda 1991, Turner & Tester 1997, Shumway et al. 2003). Similarly, cryptic mortalities of HABs on younger life stages of fish (i.e. embryos and eleutheroembryos) have not been assessed and could be significant (Tang & Gobler 2009). Mortalities on early life stages may significantly affect the recruitment of fish populations, ultimately affecting the productivity of fisheries and marine predators (Houde 1989, Rothschild 2000, Houde 2008).

In many regions in Asia, Europe and North America blooms of the toxic dinoflagellate, *Cochlodinium polykrikoides*, are now annual events (Lee et al. 2002, Gobler et al. 2008, Tomas & Smayda 2008, Kudela & Gobler 2012). The increased occurrence and persistence of harmful algal blooms has been linked with coastal eutrophication (Heisler et al. 2008), and in the United States, the linkage between HABs and eutrophication is particularly clear in sheltered coastal waters (Anderson et al. 2008). Harmful algal blooms are a major threat to coastal ecosystems and

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economies (Hoagland & Scatasta 2006), presenting significant challenges to the management and conservation of coastal living resources (Burkholder 1998, Anderson 2009, Kim 2010).

1.4 Statement of dissertation research

The overall goal of this dissertation was to evaluate the global importance of forage fish species to marine ecosystems and assess the potential impacts on these species from exposure to blooms of the harmful dinoflagellate (*Cochlodinium polykrikoides*) in coastal ecosystems. Mathematical models, field observations, and laboratory experiments were used in order to develop an understanding of the importance of forage fish in marine ecosystems and the potential lethal and sublethal effects from exposure to this HAB species. This research is timely and expected to have high relevance and impact beyond the scientific community, with the potential to influence management and policy decisions.

In Chapter 2, "Global contributions of forage fish", 72 food web models (Ecopath) from around the world were compiled in order to evaluate the role forage fish play in supporting marine predators and fisheries. This research utilized an ex-vessel price database (Sumaila et al. 2007) in order to quantify the first global estimate of the potential economic contributions forage fish species make as prey to other commercial fisheries. This research advances our understanding of the potential ecological and economic trade-offs that may be involved in the management of forage fisheries.

In Chapter 3, "Characteristics of forage fish predators and fisheries", 43 Ecopath models were explored in greater detail to determine the characteristics of forage fish predators (i.e. seabirds, marine mammals, and large predatory bony fish) globally. This chapter explored both the dietary importance of forage fish to these predators and assessed the potential for conflict with fisheries for these prey items. To do this, a variety of predator and fishery indices were calculated for each model and assessed on latitudinal and global scales. The potential utility of this work is discussed in the context of informing ecosystem-based management of forage fisheries, particularly in data poor regions.

In Chapter 4, "Toxicity of the harmful dinoflagellate, *Cochlodinium polykrikoides*, to early life stages of three estuarine forage fish", laboratory experiments were utilized to assess the potential impacts of *C. polykrikoides* clonal culture exposure to embryonic and

eleutheroembryonic (i.e. yolk-sac larvae) life stages of three forage fish species common to the U.S. East coast. This Chapter advances understanding of the ecosystem effects of *C. polykrikoides* by providing the first assessment of the potential toxicity to early life stages of fish. It has been hypothesized that impacts to early life stages of fish may be significant but go unnoticed in nature due to the relatively small sizes (Tang & Gobler 2009).

In Chapter 5, "First assessment of behavioral toxicity from sublethal exposures to harmful dinoflagellate, *Cochlodinium polykrikoides*, on swimming behavior of three estuarine forage fish species", a series of video recorded laboratory experiments were designed and conducted to evaluate the effects of exposure on fish behavior. These experiments utilized the organism tracking software (LoliTrack v.4, Loligo® Systems, Denmark) to evaluate the potential behavioral impacts of sublethal exposures of *C. polykrikoides* clonal cultures to forage fish.

The dissertation is concluded in Chapter 6, which provides a summary of key findings in the context of previous work, implications, and future directions from this research. The common theme throughout this dissertation is a focus on providing information that can be used to inform an ecosystem-based approach to forage fisheries management. In this holistic management approach, the traditional focus on a single species is reframed to take into account other ecological connections linking these species to the broader ecosystem (Brodziak & Link 2002, Pikitch et al. 2004, Link 2010). Although ecosystem-based management of forage fish species can be implemented across a range of information tiers (Pikitch et al. 2012), less precautionary management requires more information about these species as they are both highly integrated in marine ecosystems in terms of predator-prey interactions and sensitive to environmental dynamics (Pikitch et al. 2012, Essington & Plagányi 2013).

Chapter 2. Global contributions of forage fish

A version of this Chapter has been published in:

2.1 Introduction

"Forage fish" species are small or intermediate-sized pelagic species (e.g. sardine, anchovy, sprat, herring, capelin, krill, etc.) that are the primary food source for many marine predators, including mammals (Thompson et al. 1996, Pauly et al. 1998b, Weise & Harvey 2008), seabirds (Crawford & Dyer 1995, Jahncke et al. 2004, Furness 2007, Daunt et al. 2008), and larger fish (Walter & Austin 2003, Butler et al. 2010, Logan et al. 2011, Magnussen 2011). Feeding on zooplankton and phytoplankton, forage fish are important conduits of energy transfer in food webs for many marine ecosystems, from the tropics to the Earth's poles (Cury et al. 2000, Cury et al. 2003, Fréon et al. 2005, Bakun et al. 2010).

Fisheries for forage fish occur across broad latitudinal ranges (FAO 2010, 2012) and constitute a large and growing fraction of the global wild marine fish catch (Alder et al. 2008). In addition, five of the top ten fish species caught (by weight) in 2008 were forage fish species. Notably, the Peruvian anchoveta (*Engraulis ringens*) supports the largest fishery in the world (FAO 2010, 2012). Currently, nearly 90% of the global forage fish catch is used by reduction industries, which produce fish meal and fish oil (Alder et al. 2008). While economic studies of forage fish have focused primarily on their role as a directly harvested commodity (Herrick et al. 2009, Mullon et al. 2009, Tacon & Metian 2009) few have attempted to quantify the indirect economic contributions that these species provide (Hannesson et al. 2009, Herrick et al. 2009, Hannesson & Herrick 2010). Accounting for the indirect or support service values that prey species provide to other fisheries is inherently more difficult (Hannesson et al. 2009, Hannesson & Herrick 2010, Hunsicker et al. 2010), but doing so can provide important information to assess the trade-offs between exploiting forage fish and other species in the same marine ecosystem.

There has been growing scientific consensus for the application of ecosystem-based management approaches (Pikitch et al. 2004, McLeod et al. 2005, McLeod & Leslie 2009) in contrast to traditionally applied single-species approaches (Beddington et al. 2007, FAO 2010, 2012). Single-species management generally seeks to maintain populations of a target species yet ignore most ecosystem factors. Even in cases where forage fish are well managed from a single-species perspective (i.e. overfishing is not occurring), a form of "ecosystem overfishing" *sensu* Murawski (2000), can occur, whereby depleted abundance of forage fish may negatively affect the ecosystem (Gislason 2003, Coll et al. 2008). Implementing an ecosystem-based approach to the management of forage fisheries seems especially warranted (Pikitch et al. 2004, Richerson et al. 2010, Smith et al. 2011, Pikitch et al. 2012), as these species exhibit strong trophic linkages and fluctuate in abundance along with seasonal, annual, and inter-decadal variations in oceanographic forces (Barber & Chavez 1983, Francis et al. 1998, Polovina et al. 2001, Chavez et al. 2003).

Human decision-making is often influenced by comparisons of monetary values or trade-offs between different products or services (Polasky & Segerson 2009). By quantifying the value of these ecosystem products and services, such trade-offs, and the impacts of degrading ecosystems, are made more explicit (Costanza et al. 1997, Balmford et al. 2002, Barbier et al. 2011). The majority of economic analyses conducted for forage fish fisheries have been one dimensional (Herrick et al. 2009), focusing on factors or management strategies affecting the direct value of these species as a landed commodity. Only a handful of studies have enumerated the indirect values that species targeted by fisheries provide (Hannesson et al. 2009, Hannesson & Herrick 2010, Hunsicker et al. 2010, Kamimura et al. 2011). Because of their key position in marine food webs, the overall global importance of forage fish to fisheries and ecosystems has likely been significantly understated.

This study provides the first global estimate of forage fish value to commercially important marine fisheries and also enumerates the contributions of forage fish to ecosystem predator production. Data obtained from Ecopath models representing marine ecosystems around the world were synthesized for this purpose. This approach allowed for broad relationships to be detected and described by summarizing data from multiple independent studies (Gurevitch &

Hedges 1999), including information on feeding habits, production and catch rates. The contribution that forage fish species make to: 1) the diets and production of all forage fish predators within each modeled ecosystem, 2) forage fish fisheries, in terms of catch and catch value, and 3) the catch and value of other commercially targeted predator species (e.g. tunas, cod, striped bass), were estimated based on their diet dependence on forage fish. These contributions and values were compared and contrasted to evaluate the effects of model structure, ecosystem type, and latitude (Table 2.1). Finally, the relationships and properties revealed by these models together with estimates of catch values at the scale of economic exclusive zones (EEZ) and high seas areas (HSA) were used to estimate the total value that forage fish contribute to global marine fisheries.

2.2 Materials and Methods
2.2.1 Compilation & synthesis of Ecopath models

Of the more than 400 Ecopath models that have been published (Fulton 2010, Colléter et al. 2013), seventy-two were obtained and selected for this synthesis. The requirements for inclusion in this analysis were that the Ecopath models had to represent a marine or estuarine ecosystem in a relatively recent state (within the last 40 years), include at least one forage fish model group, and have all the necessary data and parameters openly available. The majority of Ecopath models used (90%, 65 out of 72) represented ecosystems within the past 30 years. Ecopath models were obtained from peer-reviewed publications (n = 33), technical reports (n = 36) and theses/dissertations (n = 3) (Table 2.1). Those that were not included failed to have at least one forage fish model group, did not have data openly available, represented older time periods (>40 years old), or a combination of all three. Collected models spanned a wide geographical range and provided relatively good global coverage of most coastal ocean areas and marine ecosystem types, with the exception of the Indian Ocean, which is poorly studied compared with other ocean areas (De Young 2006) (Figure 2.1). When available, Ecopath pedigree index information was also obtained (Christensen & Walters 2004, Christensen et al. 2005) to assess data quality of the models.

To examine the patterns in forage fish contributions and values, Ecopath models were grouped by latitude and by ecosystem type. Latitude groupings consisted of three categories:

Tropical-Subtropical (less than 30° N – less than 30° S), Temperate (greater than or equal to 30° N – 58° N and greater than or equal to 30° S – 58° S), and High latitude (greater than 58° N and greater than 58° S). Ecosystem types included: coastal upwelling ecosystems, semi-enclosed ecosystems, non-upwelling coastal ecosystems, tropical lagoon ecosystems, open ocean ecosystems, Arctic ecosystems, and Antarctic ecosystems. All models were categorized into only one ecosystem type and latitude group (Table 2.1).

In this analysis "forage fish" were defined as species that occupy an important intermediary trophic position and that retain that ecological role throughout their life span. Excluded from this definition are species that assume this role early in life but later move into higher trophic categories as they age (e.g. North Pacific hake, Blue whiting, Alaska pollock).

2.2.2 Data extraction

Model groups, catch data, diet composition matrices, biomass data, production-to-biomass ratios, and model areas (km^2) were extracted from tables in Ecopath model publications and transferred into separate Microsoft$^©$ Excel spreadsheets. When necessary, all Ecopath catch and biomass data not conforming to the standardized Ecopath units for catch (t km^{-2} yr^{-1}) and biomass (t km^{-2}) were converted.

The majority (83%) of Ecopath models in this analysis had data on total catch (landings plus discards). The remaining 17% (12 out of 72) of the models only published landings data with no estimates of discards. For these 12 models, discards were assumed to be zero in this analysis. Globally discards represent approximately 8% of the marine fisheries catch by weight but vary greatly among species and ecosystems (Kelleher 2005).

Ecopath models contain interactive "groups" which can be composed of either single or multiple species that share similar life histories or ecological functions (Polovina 1984). The original model groups, as specified by the model authors for each Ecopath model, were used. The published models generally included a list of species or taxa constituting each model group. When such taxonomic information was provided, this information was used to create an inventory of all species or other lowest taxonomic unit found in each model group and Ecopath model. A model group was classified a as a forage fish group whenever at least one forage fish

species was included in that group. For instance, if an anchovy species was a component of a larger model group called "Small Pelagics," along with gobies and juvenile mackerels, then this groups was considered as a forage fish group, even though other species in that group may not necessarily meet the definition of forage fish above. The majority (i.e. 65% or 105 out of 161) of forage fish model groups consisted entirely of forage fish species. Of the remaining 56 forage fish model groups, 30 were discerned to be dominated by forage fish species, while information on the preponderance of forage fish species was lacking for the other 26 model groups. The one exception to this classification of forage fish model groups applied to krill (Order: Euphausiacea), which were only represented as separate model groups in 9 of the 72 Ecopath models in this analysis (Table 2.1). In the few remaining Ecopath models where krill were present in the ecosystem but not as a separate model group, they were grouped into various "Zooplankton" groups. These "Zooplankton" model groups were excluded as forage fish groups in this analysis and contributions of krill from models with defined krill model groups were only included. This modeling approach may cause differences between ecosystems in terms of forage fish contributions (i.e. those that have a separate krill group and those that do not), but assumed in this analysis that if model authors grouped krill separately it was due to their perceived importance in the ecosystem. It was considered more appropriate to include krill groups as forage fish in this analysis when present rather than to completely exclude them.

2.2.3 Importance of forage fish to ecosystem predators

Forage fish predators in all models and their dependence on forage fish (% of forage fish in diet) from the respective model diet matrix were identified. Forage fish predators were defined as model groups whose diets contained any fraction of one or more forage fish model groups (i.e. diet of greater than 0% forage fish). This definition allowed for forage fish to be included as a forage fish predator, if their diet consisted of forage fish. This rarely occurred, with only 3.9% (35 out of 895) of forage fish predators also included as forage fish. Forage fish predators were then categorized into the following dependence groups: 1) Low dependence on forage fish (>0 to <25%), 2) moderate dependence (≥25 to <50%), 3) high dependence (≥50 to <75%) and 4) extreme dependence on forage fish (≥75%).

The portion of each forage fish predator's production supported by forage fish across all ecosystem models was then estimated using equations modified from Hunsicker et al. (2010). First, the total annual production (P_j, units: t km^{-2} yr^{-1}) of each forage fish predator group j in each Ecopath model was calculated using Equation (2.1), in which predator group j's biomass (B_j, units: t km^{-2}), was multiplied by that respective predator group's production-to-biomass ratio ($P\,B^{-1}$, units: yr^{-1}).

$$P_j = B_j \left(\frac{P}{B}\right)_j \tag{2.1}$$

Second, the portion of each predator group's total annual production ($P_{i,j}$) supported by forage fish prey groups (i) was found by multiplying predator group j's respective diet dependence on forage fish ($D_{i,j}$) by P_j using Equation (2.2).

$$P_{i,j} = D_{i,j} P_j \tag{2.2}$$

The total support service contribution of forage fish to ecosystem predator production (S_z) therefore was found using Equation (2.3), as the product of ($D_{i,j}$) and (P_j) summed over all forage fish groups (i) and predator groups (j) in an ecosystem.

$$S_Z = \sum_j \sum_i D_{i,j} P_j \tag{2.3}$$

Hunsicker et al. (2010) showed that $D_{i,j}$ is equivalent to the contribution of prey group i to predator group j's production ($P_{i,j}$) when assimilation and energy content of prey items are roughly equivalent. In the absence of detailed data on these variables, it was assumed they were equal to one another but note that this analysis underestimates $P_{i,j}$, because of the generally high energy content of forage fish species (Van Pelt et al. 1997, Anthony et al. 2000) compared to most predators. Thus, these estimates for the support service contribution of forage fish to ecosystem predator production can be considered conservative in this regard.

2.2.4 Direct and support service contributions of forage fish to commercial fisheries

The contributions of forage fish to fisheries in terms of both catch (t km^{-2} yr^{-1}) for all 72 Ecopath models and catch value (2006 USD km^{-2} yr^{-1}) for a subset of models that had adequate taxonomic information (n = 56) were calculated. Ecopath models were grouped into categories

based on ecosystem type and latitude of the model (Table 2.1). A global ex-vessel price database, developed by Sumaila et al. (2007), was used to obtain ex-vessel "real" price data for all fished species in these Ecopath models. Ex-vessel "real" price is defined as the actual prices that fishermen receive for their products before processing and is hereafter simply referred to as price. In this analysis, we use "value" to refer to ex-vessel fish price times quantity (gross returns) and not economic profit (net returns).

Total catch data for every country participating in fisheries in a respective Large Marine Ecosystem (LME) in 2006 were obtained from the Sea Around Us project LME database (Watson et al. 2004; www.seaaroundus.org), and the ex-vessel price database was used to compile country specific ex-vessel price data for every species in the 56 models. Information on every fishing country in each LME and their respective total catch was accessed on the Sea Around Us project LME database website (www.seaaroundus.org). To account for differences in prices between countries operating in a given LME, a weighted average based on the total catch in 2006 of all participating countries within that LME was calculated. When model groups consisted of two or more species, the ex-vessel price for the model group was found by averaging the ex-vessel prices for all respective species within, which were each weighted by the catches of participating countries. These averaged ex-vessel model group prices were used to calculate fisheries value (2006 USD km^{-2} yr^{-1}) for each respective model group in all 56 Ecopath models.

For small geographic areas (e.g. estuaries, lagoons, and small coastal areas), it was assumed that only the country surrounding these waters fished them. This assumption was made because detailed information about which specific countries fish within an Ecopath model area is not usually published. For the few Ecopath models that were located outside a defined LME area (e.g. Central North Pacific Ocean, Central Atlantic Ocean, and Eastern Subtropical Pacific Ocean), participating fishing countries were assumed to be those nearest to, and surrounding, the model locations. Ecopath models of island countries and territories that fell outside of LME boundaries (e.g. the Azores Archipelago) were assumed to be fished only by that country, or the country of which it is a territory.

Forage fish catch was estimated by summing the catch of all forage fish model groups in each respective ecosystem model. Catch value (2006 USD km^{-2} yr^{-1}) was estimated for each respective forage fish model group by multiplying the catch (t km^{-2} yr^{-1}) and the respective ex-vessel price (2006 USD t^{-1}) (Sumaila et al. 2007). Similarly, catch values for all forage fish model groups were summed to find the total forage fish catch value (2006 USD km^{-2} yr^{-1}) in each Ecopath model. The support service contributions of forage fish to the catch (S_C) and catch value (S_V) of other commercially targeted model groups was estimated using Equation (2.3), except that the predator group's total annual production (P_j) was replaced by the catch (C_j, Equation 2.4) and catch value (V_j, Equation 2.5) of each predator group j.

$$S_C = \sum_j \sum_i D_{i,j} C_j \qquad\qquad\qquad (2.4)$$

$$S_V = \sum_j \sum_i D_{i,j} V_j \qquad\qquad\qquad (2.5)$$

2.2.5 Forage fish contribution to global fisheries value

Forage fish species contribute to the value of global fisheries in two important ways: 1) by their direct catch value and 2) by their support service as prey to the value of other commercially targeted species. Using forage fish value estimates for these contributions from each Ecopath model, extrapolations to Exclusive Economic Zone (EEZ) or High Seas Area (HSA) regions were made to derive global estimates. EEZs and HSAs were used because independent estimates of forage fish catch values were available at this scale (Sumaila et al. 2007) to complement the values estimated in Ecopath models. It was assumed that a single Ecopath model representing an area within an EEZ or HSA region provided a reasonable depiction of the relationship between the support service value of forage fish and the total fisheries value for the entire region. A breakdown of the actual area covered by our Ecopath models as a percentage of the total EEZ/HSA area or the total Inshore fishing area (IFA) can be found in Table 2.2. The IFA is defined by the Sea Around Us Project database (www.seaaroundusproject.org) as the area between the shoreline and whichever comes first, either the 200 m bathycline or a distance of 50 km from the shoreline. The majority of the global marine fisheries catch value (78%) and forage fish catch value (97%) is derived from IFAs (Sumaila et al. 2007, www.seaaroundusproject.org). A summary of Ecopath model coverage in

13

terms of EEZ/HSA or IFA area and fisheries value is provided in Table 2.3. When multiple Ecopath models were available for a given EEZ or HSA region, average values weighted by the geographic area covered by each ecosystem model were used. Global forage fisheries value was quantified by summing the value of forage fish across all EEZs and HSAs in the Sea Around Us project database. The majority of forage fish species in these databases were separated into two commercial groups, "Herring-likes" and "Anchovies". It was assumed that the total direct forage fish catch value for each respective EEZ and HSA was the sum of these two commercial groups. When data on "Herring-likes" and "Anchovies" were missing from this database, data available for forage fish categorized by species group were used. This method may slightly underestimate forage fisheries value, as it did not include some forage fish species that were grouped into other non-forage fish commercial groups.

To estimate the global support service value of forage fish to other commercially targeted species, the values estimated for each Ecopath model were extrapolated to each corresponding EEZ and HSA region. To do this, an Ecopath value ratio (EVR) was calculated for each Ecopath model with value data available using Equation (2.6). In Equation (2.6), the catch value of forage fish predators supported by forage fish (Sv) was divided by the total fishery catch value (y) of the Ecopath model, excluding non-cephalopod, non-krill invertebrates (e.g. other decapods, bivalves). By assuming that EVRs found in Ecopath models are representative of the larger EEZs or HSAs in which they are located, the total support service value ($\$Supportive$) of forage fish in each EEZ and HSA was calculated. Using Equation (2.7) the respective EVR for an EEZ or HSA was multiplied by the total fishery catch value (excluding non-cephalopod, non-krill invertebrates) for that area from the Sea Around Us database ($\$SAUP$).

$$EVR \; = \; \frac{Sv}{y} \qquad\qquad\qquad\qquad (2.6)$$

$$\$Supportive \; = \; EVR \times \$SAUP \qquad\qquad (2.7)$$

Ecopath models were available for 25% (64 out of 257) of the world's EEZs and HSAs, which represents 33% of the total EEZ/HSA area (Table 2.3). In the majority (36 out of 64) of these EEZ/HSA areas, Ecopath model coverage was greater than 50% of the respective EEZ/HSA area (Table 2.2). These EEZ/HSAs constitute 39% of the global marine catch value

(2006 $USD) excluding non-cephalopod and non-krill invertebrates (i.e. other decapods, bivalves) and 53% of the global forage fish catch value (2006 $USD) (Table 2.3). Model coverage of IFAs was even greater at 47% of the total area (km^2) (Table 2.3). An additional 86 EEZs and HSAs (Table 2.2) which did not have Ecopath models, were included under the assumption that the Ecopath model in the EEZ or HSA immediately adjacent was representative of that neighboring EEZ or HSA. These EEZs and HSAs represented an additional 28% of the global forage fish catch value to fisheries. The remaining 107 EEZs or HSAs did not have Ecopath models or an adjacent neighbor with an Ecopath model (e.g. isolated islands) and represented only 19% of the global forage fish value to fisheries. In these EEZ/HSA areas, an EVR based on the average of EVRs from other Ecopath models in the same latitudinal group was applied (Table 2.4). All values were calculated as ex-vessel price values in 2006 $USD and all support service values and forage fisheries catch values were summed across all EEZs and HSAs. This produced an estimate of forage fish contribution to global fisheries value.

2.3 Results
2.3.1 Quality of Ecopath models

Ecopath pedigree indices (Christensen & Walters 2004) were available for 22 models (Table 2.1). The Ecopath pedigree index varies with the quality of data within Ecopath models, and values can range from 0 (not reliable) to 1 (highly reliable) (Christensen & Walters 2004, Christensen et al. 2005). Ecopath pedigree indices in this analysis ranged from 0.295 to 0.820 with the majority (55%, 12 out of 22) exceeding 0.5 (Table 2.1). Differences were observed in pedigree indices of models published in peer-reviewed journals (Ecopath pedigree mean = 0.625, median = 0.638, n = 11) and technical reports (Ecopath pedigree mean = 0.450, median = 0.408, n = 11). No indices from models in this analysis were in the poorest quality level grouping wherein data are considered to be no better than guesses (<0.2; (Christensen & Walters 2004, Christensen et al. 2005). Moreover, the average and median pedigree indices observed in this study (0.518 and 0.537, respectively) were substantially higher than those for other studies (0.441 and 0.439, respectively)(Morissette et al. 2006, Morissette 2007).

2.3.2 Extent of predator dependence on forage fish

Seventy-five percent (54 out of 72) of the Ecopath models used in this analysis had at least one model group that was highly (>50% but <75% of diet) or extremely dependent (≥75% of diet) on forage fish. Twenty-nine percent (21 out of 72) of the models included at least one extremely dependent predator group. Extremely dependent predators were present across all latitude groups and ecosystem types, with the exception of open ocean ecosystems. These predators accounted for only 5.8% (52 out of 895) of all forage fish predators and consisted of fishes (n = 30), seabirds (n = 12), marine mammals (n = 9), and one species of squid (*Loligo gahi*). Amongst conspecific predator groups however, seabirds had the highest percentage of extremely dependent predators, with 19% (12 out of 62) of all seabird predators having diets ≥75% forage fish. Extremely dependent predators groups were most commonly found in upwelling and Antarctic ecosystem types, with an average of 2 and 5 extremely dependent predators per model, respectively. Many of these extremely dependent predator species were also listed on the IUCN Red List (Table 2.5).

The relative frequency of various levels of forage fish dependencies and how they varied across ecosystem types were evaluated by combining data from all models. Pooled data across all ecosystem models indicated that on average, 49% of all predator groups in these models relied on forage fish for at least 10% of their dietary requirements (Figure 2.2). Forage fish predators that were highly or extremely dependent on forage fish accounted for 16% of all predator groups in marine ecosystem models on average. Predators with diets consisting of more than 90% forage fish were also found but represented fewer than 5% of all predator groups in this analysis.

When comparing across ecosystem types, Antarctic ecosystem models generally had the greatest proportion of forage fish predators in their models for any level of forage fish dependence compared to other ecosystem model types (Figure 2.2). Upwelling ecosystems had the second-highest percentage of predators with 90% forage fish dependence levels. Tropical lagoon ecosystem types had the lowest proportion of predators for a given forage fish dependence level (Figure 2.2).

2.3.3 Support service contribution to ecosystem predator production

The total predator production (t km^{-2} yr^{-1}) supported by forage fish varied greatly among the 72 models in this analysis (Figure 2.3). Supported predator production was largest for two upwelling ecosystem models, the northern California Current model and central Chile model, and one non-upwelling coastal ecosystem (Falkland Islands model). Forage fish contributed 52 t km^{-2} yr^{-1} and 17 t km^{-2} yr^{-1} to predator production in northern California Current and central Chile models respectively, and the contribution in the Falkland Islands model was 18.9 t km^{-2} yr^{-1}. When the contribution of krill to the production of other forage fish (e.g. krill, sardines, anchovies) was removed in the northern California Current and Falkland Islands models, the support service to predators dropped to 32 t km^{-2} yr^{-1} and 3.3 t km^{-2} yr^{-1} respectively.

Across ecosystem types, the greatest support service contribution of forage fish to predator production was found in upwelling and Antarctic ecosystems (Figure 2.4a). The support service contribution to predator production in both these ecosystem types exceeded 9 t km^{-2} yr^{-1} and were more than three times greater than values seen for Arctic ecosystems and non-upwelling coastal ecosystems, and more than an order of magnitude greater than open-ocean, tropical lagoon, and semi-enclosed ecosystem types (Figure 2.4a). In terms of latitude groupings (with upwelling ecosystems excluded), the greatest support service contributions to predator production were found in high latitude regions (3.79 t km^{-2} yr^{-1} ± 1.23 SE), followed by temperate latitudes (1.81 t km^{-2} yr^{-1} ± 0.59 SE), and finally tropical-subtropical latitudes (1.18 t km^{-2} yr^{-1} ± 0.17 SE; Figure 2.4b). Upwelling ecosystem models were separated from the latitude groupings due to the dominant roles forage fish catches play in these ecosystems.

2.3.4 Importance of forage fish to commercial fisheries

Forage fish catch varied greatly among models examined, both in tonnage and ex-vessel price value. In some models, no forage fish catch was reported (e.g. Central Atlantic Ocean), while others had extremely large forage fish catches (e.g. Sechura Bay, Peru). The highest forage fish catches were found in the Humboldt Current models where the Peruvian anchoveta fishery operates. Of the three Humboldt Current models, the Sechura Bay (Peru) model had an extraordinarily high level of forage fish catch (81 t km^{-2} yr^{-1}) valued at $35,497 (USD km^{-2} yr^{-1}), whereas in the northern Humboldt Current models for both El Niño and La Niña periods, forage

fish catches were 20 t km^{-2} yr^{-1} ($934 USD km^{-2} yr^{-1}) and 39 t km^{-2} yr^{-1} ($2,020 USD km^{-2} yr^{-1}) respectively.

Forage fish contributed important support to other commercial fisheries in all models that contained such fisheries. Of the ecosystems examined, forage fish were most important as prey, in terms of tonnage, to commercial fisheries in central Chile (3.82 t km^{-2} yr^{-1}), Prince William Sound (pre-oil spill model; 3.58 t km^{-2} yr^{-1}) and the northern California Current (3.13 t km^{-2} yr^{-1}; Figure 2.5). In terms of value, forage fish provided the greatest support service to fisheries in the Prince William Sound model (pre-oil spill model) at a value of $5,942 USD km^{-2} yr^{-1}, followed by the Chesapeake Bay at a value of $3,095 USD km^{-2} yr^{-1}. The high support service values in these ecosystems were due to the large contribution of forage fish to the diets of salmon (*Oncorhynchus* spp.) in Prince William Sound and striped bass (*Morone saxatilis*) in Chesapeake Bay, both of which had relatively high ex-vessel price values.

In 13 out of 56 models, 100% of the total forage fish value was derived from support to other fisheries (i.e. there were no forage fish fisheries reported in these 13 ecosystems). In more than half the models (30 out of 56), the value of the fisheries supported by forage fish was greater than the value of forage fish catch (Figure 2.6).

2.3.5 Comparisons across latitude groups and ecosystem types

The largest forage fish catches were found in the tropical-subtropical latitude group (4.95 t km^{-2} yr^{-1} ± 2.5 SE) and decreased monotonically toward polar regions. In contrast, the level of other commercial catch supported by forage fish was lowest in the tropical-subtropical latitude group (0.23 t km^{-2} yr^{-1} ± 0.05 SE) but greater in temperate (0.63 t km^{-2} yr^{-1} ± 0.2 SE) and high latitude ecosystems (0.35 t km^{-2} yr^{-1} ± 0.29 SE). Again, upwelling ecosystem models were separated from these latitude groupings, as forage fish catches play a dominant role in these ecosystems. Temperate models had the highest forage fish fisheries catch compared with the remaining two latitude groups (Figure 2.7a). Forage fish catch value (excluding upwelling ecosystems) was greatest in the tropical-subtropical latitude group and diminished poleward (Figure 2.7b). The support service provided by forage fish for other commercial fisheries, in both

catch and catch value, increased poleward so that it was equivalent (in catch) or exceeded (in catch value) the forage fish catch or catch value in high latitudes (Figure 2.7).

Forage fish catch (t km^{-2} yr^{-1}) was highest in upwelling ecosystems (Figure 2.8a), exceeding that of all other ecosystem types combined by a factor of four. Forage fish catch exceeded the catch of other model groups that preyed on forage fish for all ecosystem types (Figure 2.8a). Similarly, forage fish had the highest catch value in upwelling ecosystems at $5,660 USD km^{-2} yr^{-1} ± $4,980 SE (Figure 2.8b). Other ecosystem types had substantially lower forage fish catch values, each contributing less than $830 USD km^{-2} yr^{-1}. The value of forage fish catches was smallest in high latitude Arctic and Antarctic ecosystems ($184 USD km^{-2} yr^{-1} and $149 USD km^{-2} yr^{-1}, respectively). In contrast, the support service value of forage fish was greatest in the Arctic ecosystems (HL, mean = $706 USD km^{-2} yr^{-1}) – over 3.5 times greater than the forage fish value for that ecosystem type (Figure 2.8b).

2.3.6 Global estimate of forage fish value to fisheries

The estimated total ex-vessel price value of forage fish to global commercial fisheries was $16.9 billion ($USD). This estimate combined a global forage fish fishery value of $5.6 billion (33%, USD) with a support service value to other fisheries of $11.3 billion (67%, USD). This value represents nearly 20% ($16.9b/$85b) of the ex-vessel catch values of all world fisheries, estimated at between $80-85 billion USD yr^{-1} (Sumaila et al. 2007, FAO 2010). Importantly, the value of commercial fisheries supported by forage fish (e.g. cod, striped bass, salmon, etc.) was twice the value of forage fish fisheries at a global scale. Calculated Ecopath value ratios (EVRs) for each model can be found in Table 2.6, while latitudinal averages of EVRs can be found in Table 2.4.

2.4 Discussion

It is recognized that using Ecopath models, as for any mathematical representation of an ecosystem, has certain limitations. However, this approach was built around the idea that, within the constraints of the model assumptions, averaging across many models will at least reduce the effects of stochastic uncertainty. Ecopath models provide only a single spatial and temporal representation of an ecosystem and they contain numerous assumptions whose consequences are often impossible to assess and which could be important. This means, at the very least, that they

do not capture changes in ecosystem dynamics and fisheries effort over space and time. Models are constructed based on data availability and the author's understanding of the ecosystem and research objectives, allowing for a gradient in model complexity and quality. The models contain simplistic diet information of predators included in the models and that needs to be considered when interpreting or using the results of this study. For example, some Ecopath models lacked predators that are known to prey on forage fish, and in other cases, investigators pooled individual predator species together into a single trophic group. Nearly 30% (21 out of 72) of the models in this study did not have any seabird model groups, while 33% (24 out of 72) did not have a marine mammal group. Estimates for predator production therefore are likely to be conservative, since they were not able to capture the importance of forage fish to these predators not included in the models. Likewise, aggregating predator species into model groups results in an averaged diet dependence on forage fish for the model group, which may mask high diet dependence for one or more individual species in that group. Averaging diet dependence for a single species over a large geographic area may also mask high diet dependencies that occur on smaller spatial or temporal scales. Validating every model to determine how well it represents its respective ecosystem and biological components was beyond the scope of this analysis, but Ecopath pedigree index information for a subset of models show that the majority used in this analysis are of acceptable quality (Table 2.1). Using published models provided this work with a large number of models covering the widest range of ecosystems and latitudes possible.

Here information on catches, catch values and food web connections were used to estimate the global contribution of forage fish to fisheries and ecosystems. While the importance of forage fish varied geographically, it was clear that these species are of critical importance to many predators, including humans. This approach is considered as a reliable and relatively quick way of assessing the importance of forage fish in marine ecosystems and fisheries around the world. Ecopath models in this analysis covered 33% of the total EEZs and HSAs and covered 47% of the IFA (Table 2.2), which is where 97% of the global forage fisheries catch value is derived (Sumaila et al. 2007). It is acknowledged that geographic coverage was limited in the Indian Ocean. Although EEZ and HSA areas in the Indian Ocean account for 20% of the total EEZ and HSA area, they represent less than 15% of the total fisheries catch value (excluding non-cephalopod or non-krill invertebrates) and less than 12% of the total forage fish catch value.

Furthermore, Indian Ocean EEZ and HSA areas accounted for less than 10% of the total global supportive value of forage fish. More robust fisheries information from this data-poor region (De Young 2006) would benefit future analyses.

At the global scale the supportive value of forage fish to fisheries greatly exceeded their direct commodity value. The estimated total ex-vessel value ($16.9 billion USD annually) is likely an underestimate, because it does not take into account the contribution of forage species to early life history stages of predators that are not yet of commercial catch size (e.g. juvenile cod, juvenile striped bass). This analysis also did not include the contributions of species that are considered forage fish only during juvenile life stages (e.g. Alaska pollock etc.). Accounting for these types of forage species would increase estimates of support to ecosystem predator production and marine fisheries in certain ecosystems. More importantly, the ex-vessel value of commercial fisheries is only one of many other indicators of the economic contributions of forage fish, and thus is clearly an underestimate of the total economic worth of these species. For instance, the potential economic value of forage fish to recreational fisheries, to ecotourism (e.g. the whale watching industry is estimated at $2.5 billion 2009 USD annually (Cisneros-Montemayor et al. 2010)), as bait for fisheries, and to the provision of other ecosystem services such as water filtration remains largely unexplored.

Forage fish are integral to marine food webs as prey for a wide variety of higher trophic-level species. For many predators, forage fish constitute a substantial percentage of their diet, possibly making them vulnerable to reductions or fluctuations in forage fish biomass. Many extremely dependent predators identified in this study were species listed on the IUCN Red List as "Near Threatened", "Vulnerable", or "Endangered" (Table 2.5). These predators were commonly found in upwelling ecosystems, where empirical evidence shows that changes in forage fish abundance—caused by fishing, the environment, or a combination of both—negatively impact predator reproduction (Sunada et al. 1981, Becker & Beissinger 2006), breeding (Crawford & Dyer 1995, Cury et al. 2011) abundance (Crawford & Jahncke 1999, Jahncke et al. 2004) and carrying capacity (Crawford et al. 2007). This analysis has identified ecosystems that are likely to have highly to extremely dependent forage fish predators, and may

assist in ecosystem-based management efforts that consider both commercial fisheries and effects to threatened or endangered species.

The first global estimates of the importance of forage fish as support for predators in marine ecosystems is provided in this study. Quantifying forage fish catch, support service to other commercially targeted predators, and support to all other ecosystem predators allows for identification of potential trade-offs that may occur among uses (Figure 2.9) Competition for the use of forage fish biomass among ecological and fisheries interests can result in trade-offs, which can lead to conflicts in the management of forage fish. This is especially important as forage fish are an increasingly valued commodity (Naylor et al. 2009, Tacon & Metian 2009, 2013) and provide fundamental ecological support to many other species. Taking a holistic viewpoint of their value is a step towards quantification of the overall contributions forage fish make to marine ecosystems and to the global economy. A challenge that remains for fisheries managers and policy makers is determining acceptable levels of catch that account for the roles forage fish play in the larger marine environment.

The management of trade-offs in marine ecosystems can often be challenging (Okey & Wright 2004, Cheung & Sumaila 2008, Salomon et al. 2011), but accounting for trade-offs is important and can lead to more sustainable levels of exploitation without compromising ecosystem integrity (Okey & Wright 2004). Ultimately, accounting for trade-offs between forage fish fisheries and conservation goals will require knowledge and understanding of the sensitivity to which commercially targeted and non-commercial predator species respond to fisheries induced changes in forage fish abundance. A combination of both modelling (Okey & Wright 2004, Cheung & Sumaila 2008, Smith et al. 2011) and empirical (Read & Brownstein 2003, Brodziak et al. 2004) methods will likely be required to fully understand trade-offs in forage fish management.

2.5 Chapter 2 Figures
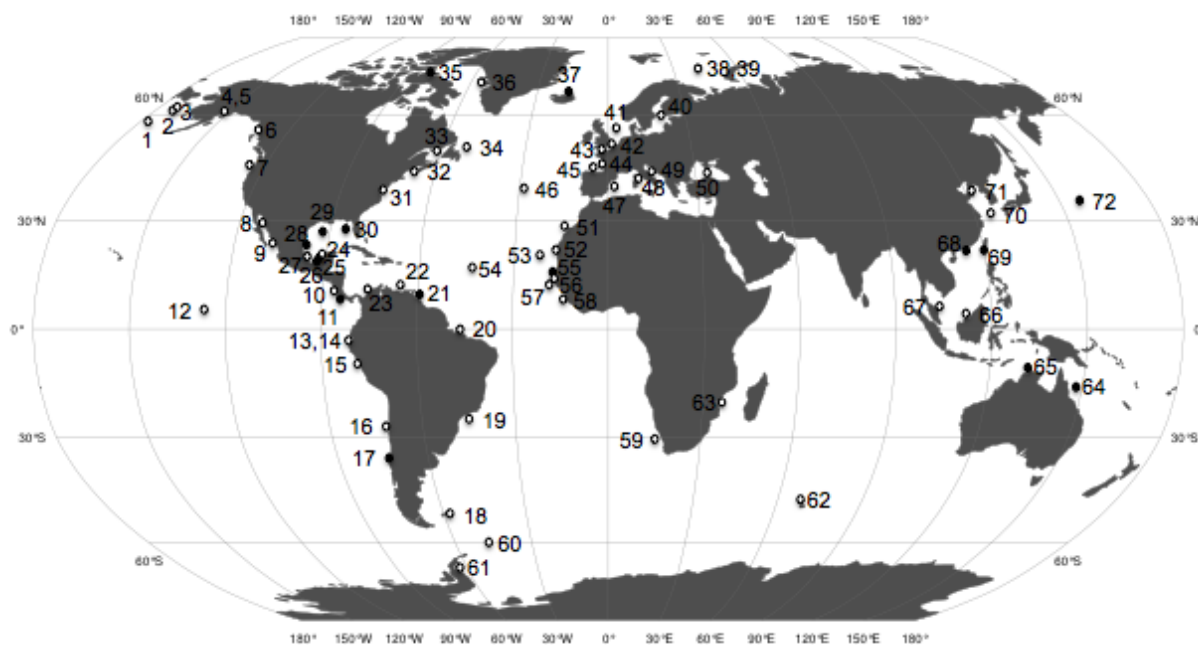
Figure 2.1 Approximate locations of the 72 Ecopath models used in this synthesis. Ecopath models where value could (white circles) and could not (black circles) be calculated. Model numbers correspond to Table 2.1.
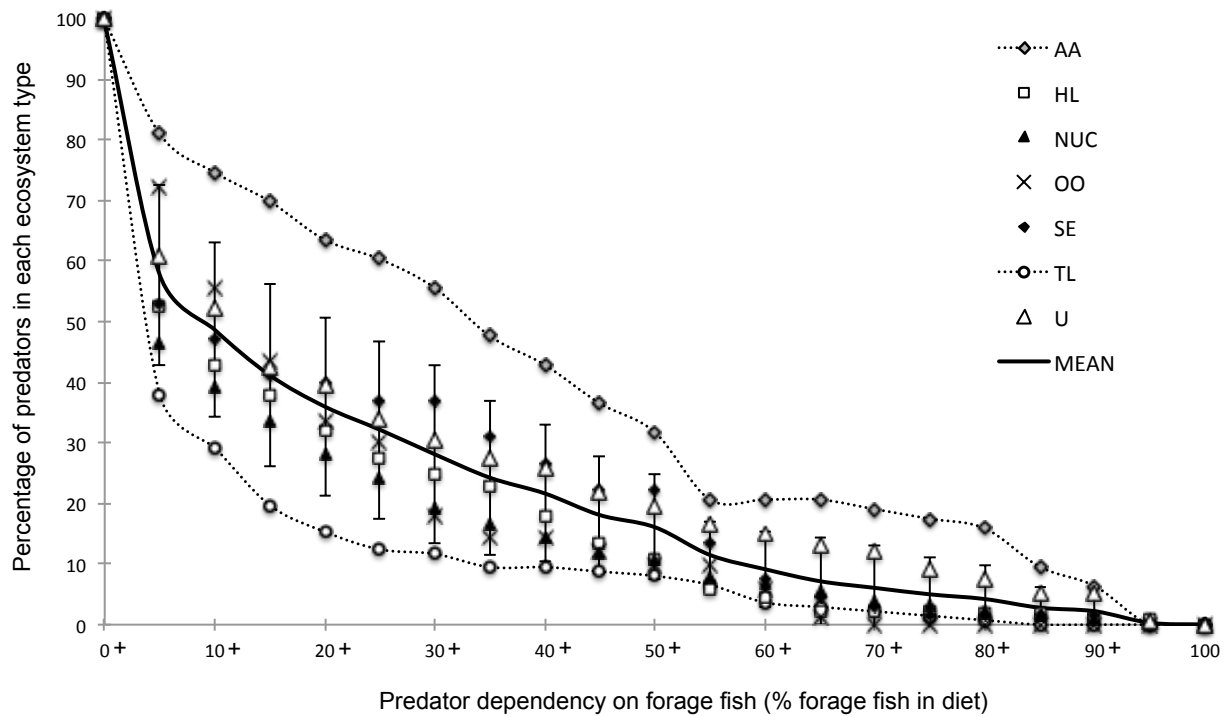
Figure 2.2 Percentage of forage fish predators in analyzed ecosystems (n = 72) and their dependence on forage fish (% forage fish in diet). Solid line represents the Mean ± SD for all predators in this analysis. Ecosystem types: AA = Antarctic, OO = open ocean, U = upwelling current, HL = Arctic high latitude, SE = semi-enclosed, NUC = non-upwelling coastal, TL = tropical lagoon.
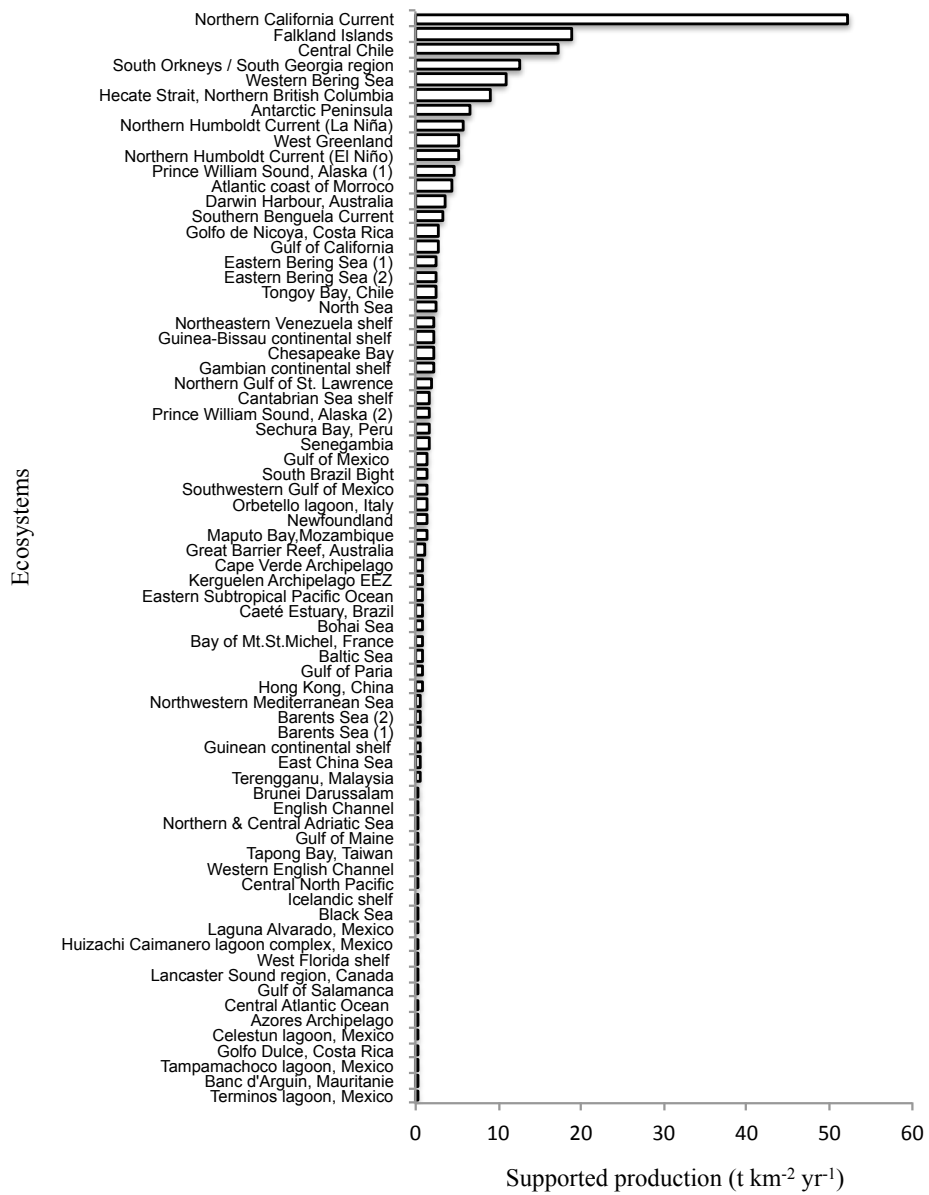
Figure 2.3 Support service of forage fish to ecosystem predator production across all Ecopath models in this analysis (n = 72).
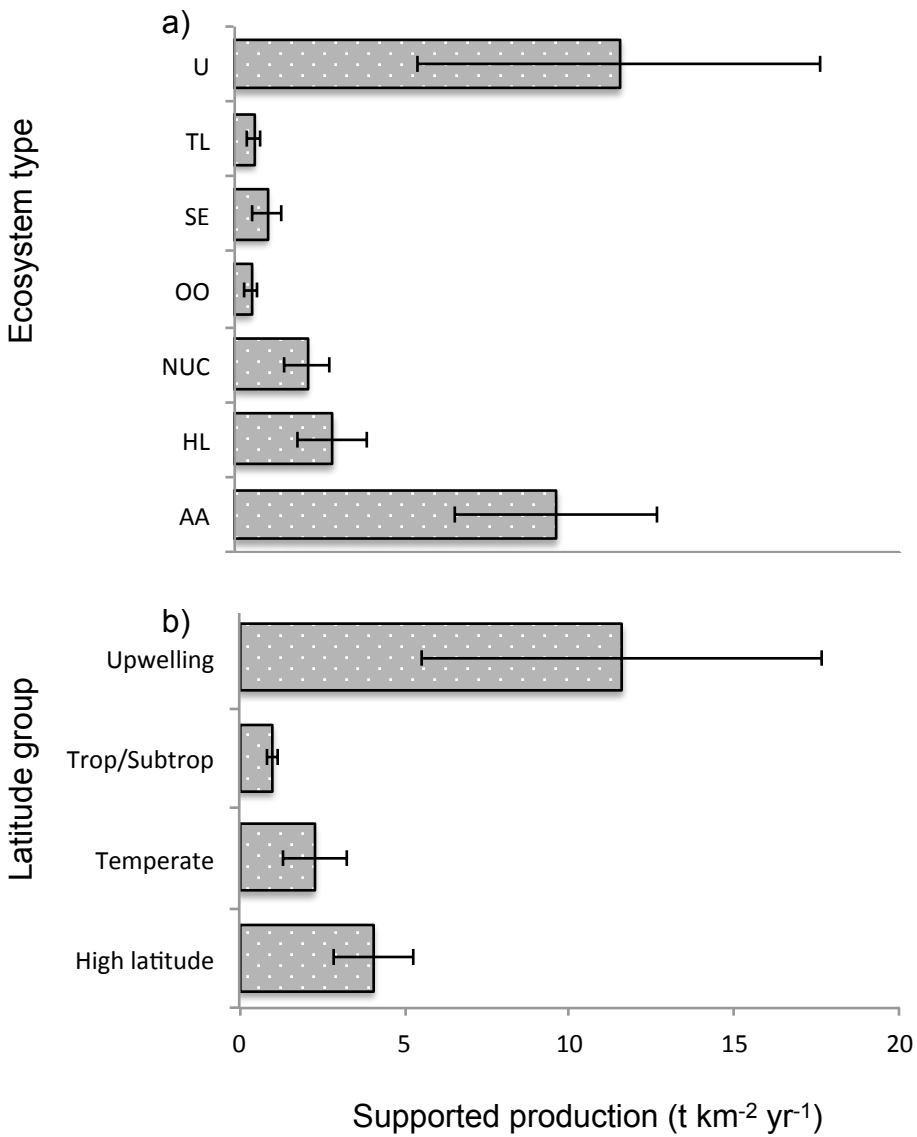
Figure 2.4 Mean forage fish contribution to (non-commercial) ecosystem predator production by ecosystem type (a) and latitude grouping (b) with standard error plotted. Ecosystem types: U = upwelling current, TL = tropical lagoon, SE = semi-enclosed, OO = open ocean, NUC = non-upwelling coastal, HL = Arctic high latitude, and AA = Antarctic.
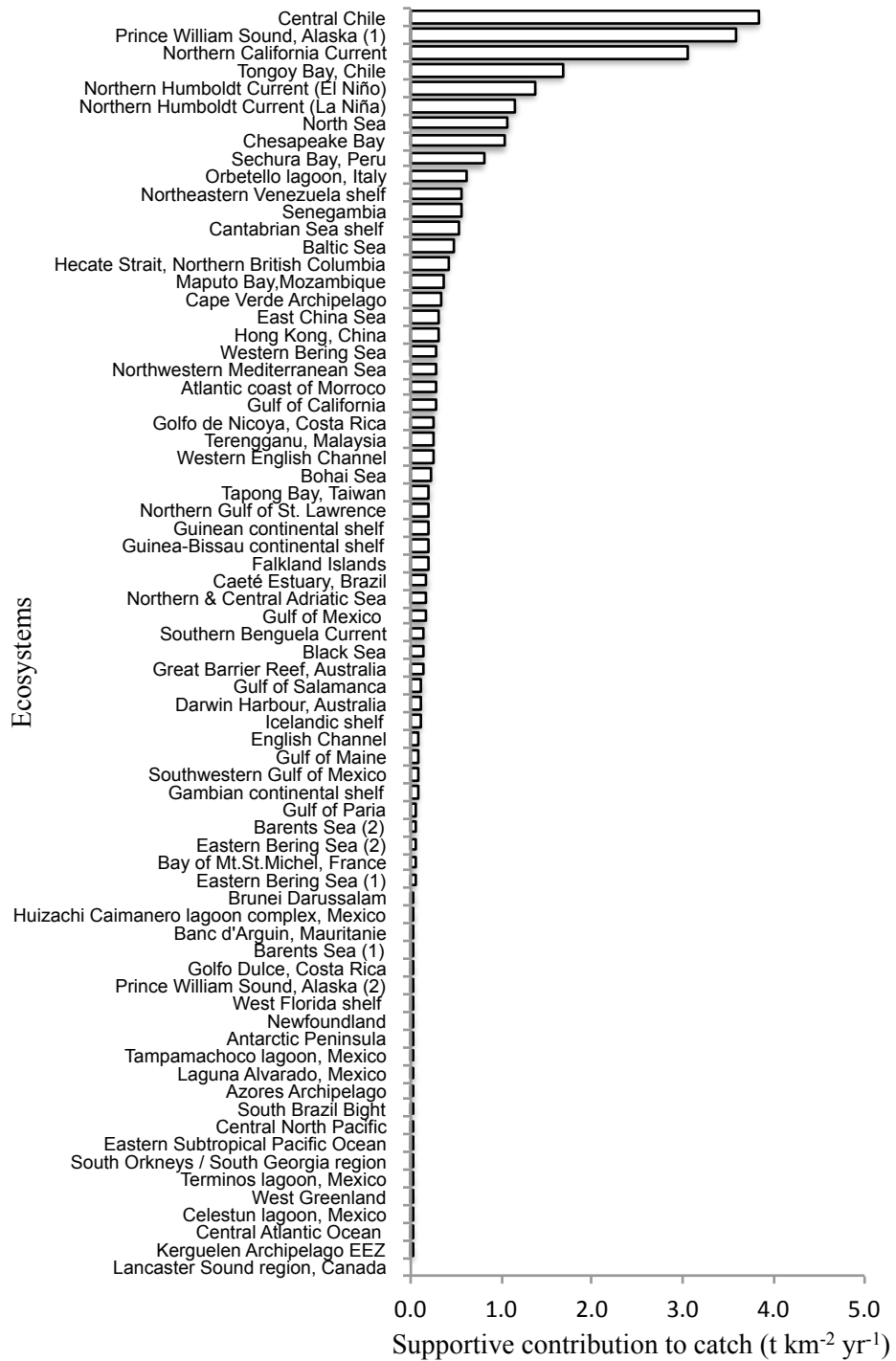
Figure 2.5 Support service contributions of forage fish to other fisheries catch across all Ecopath models (n = 72).
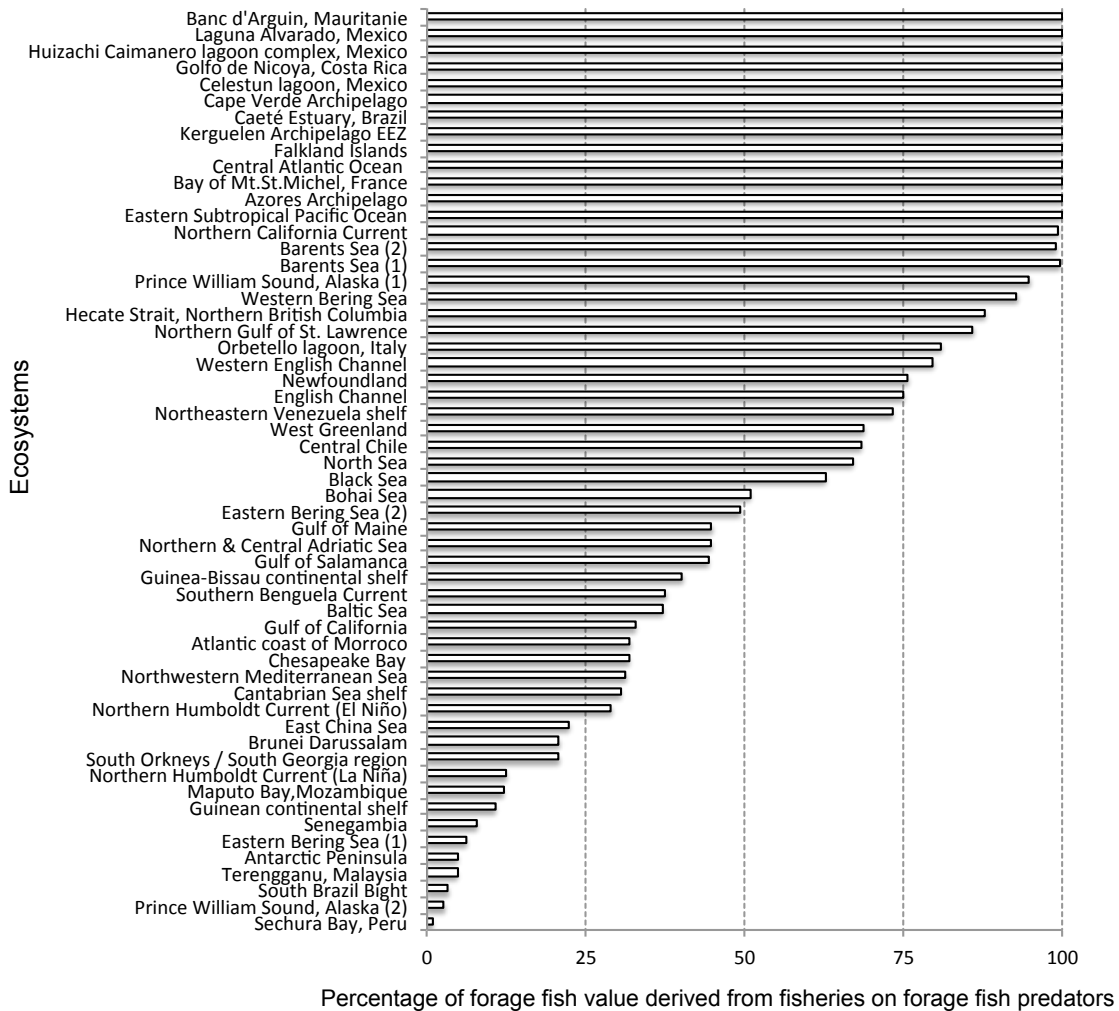
Figure 2.6 Percentage of total forage fish values (forage fish fisheries value + support service value to other fisheries) across Ecopath models (n = 56) derived from forage fish support service to other commercial fisheries. Ecosystems with 100% support service to other commercial fisheries do not have active forage fish fisheries in their respective ecosystem model.
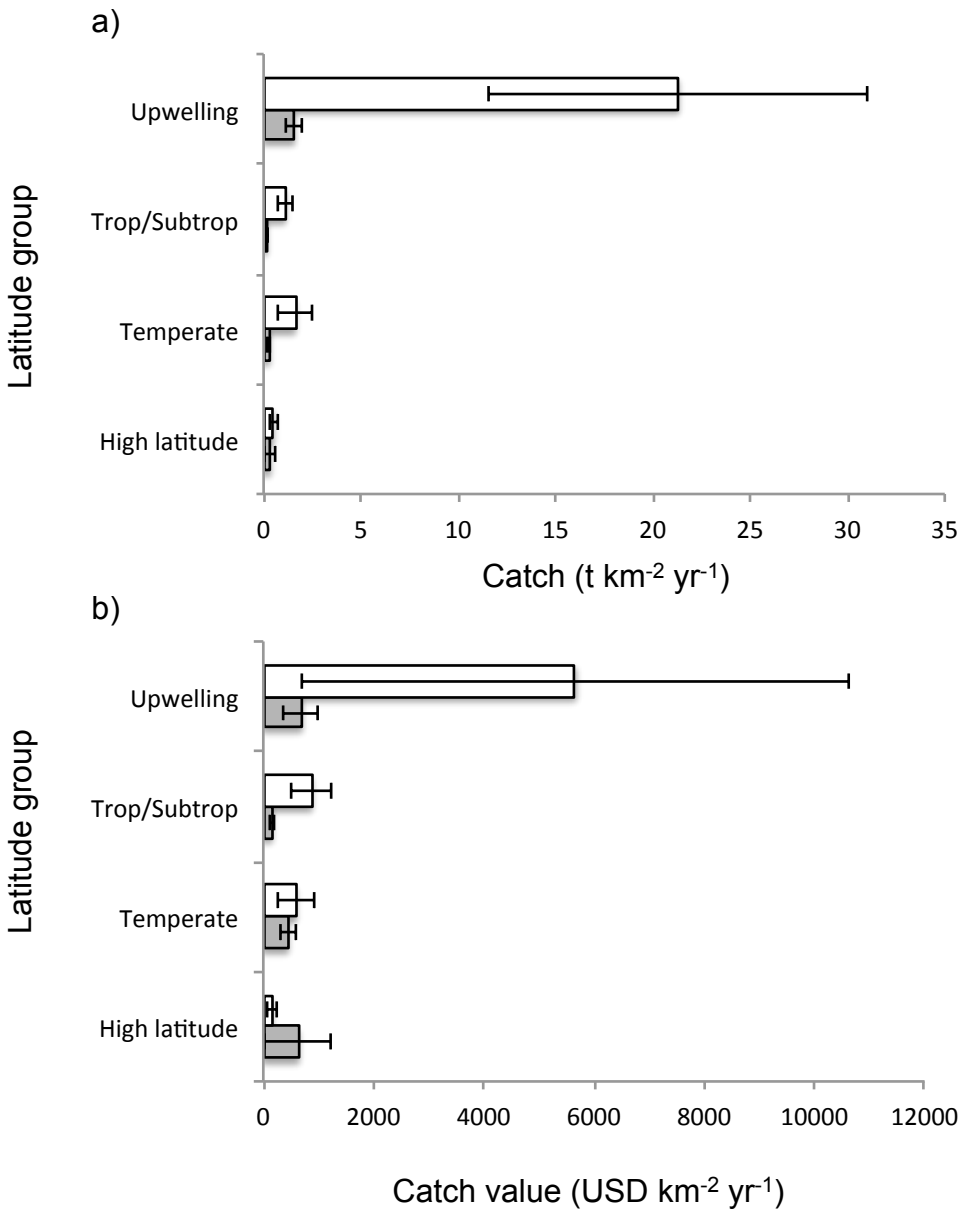
Figure 2.7 Mean catch (a) and mean catch value in 2006 USD (b) of forage fish (white bars) and mean supportive contribution of forage fish to other species' catch and catch value (grey bars), by latitude group. Bars indicate standard error. Upwelling ecosystem models were separated out to more clearly demonstrate latitudinal patterns.
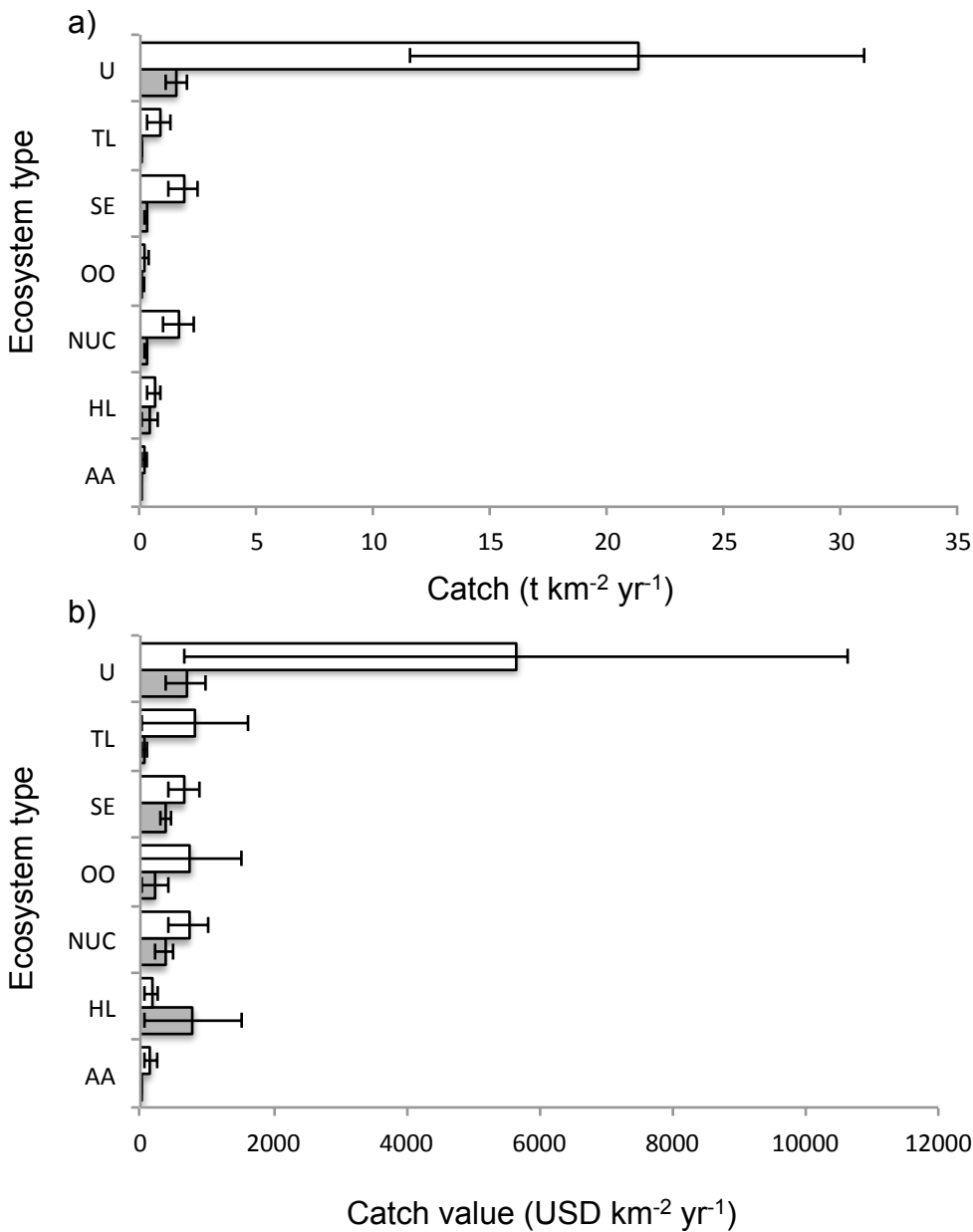
Figure 2.8 Mean catch (a) and catch value in 2006 USD (b) of forage fish (white bars) and mean supportive contribution of forage fish to other species' catch and catch value (grey bars). Bars indicate standard error. Ecosystem types: U = Upwelling current, TL = Tropical lagoon, SE = Semi-enclosed, OO = Open ocean, NUC = Non-upwelling coastal, HL = Arctic high latitude, and AA = Antarctic.
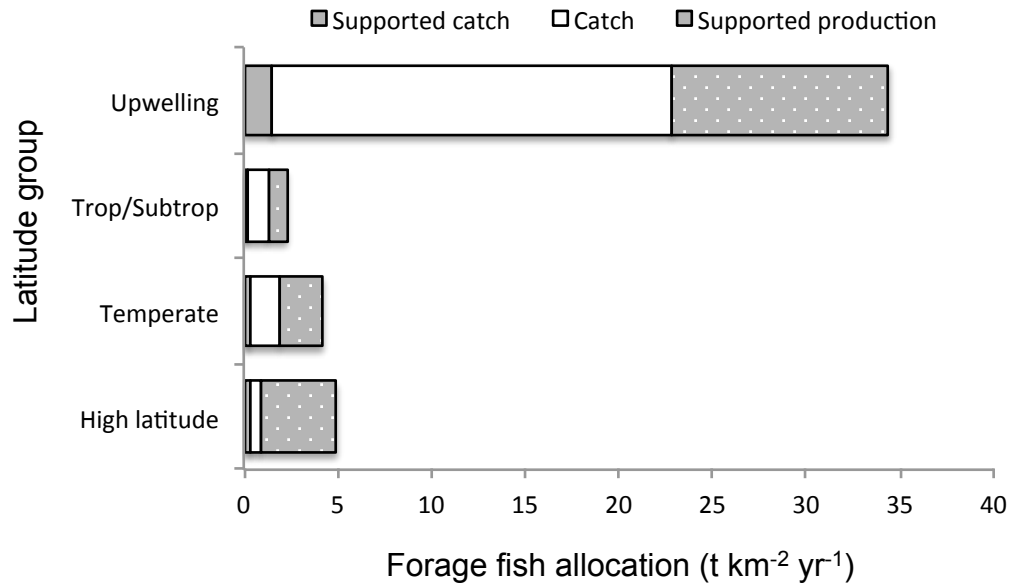
Figure 2.9 Forage fish allocation across latitude groups in terms of support service to fisheries (grey bars), forage fish catch (white bars), and support service to ecosystem predator production (dotted grey bars).

2.6 Chapter 2 Tables

Table 2.1 List of the 72 Ecopath models used in this synthesis. MG = Model groups, P = Predator model groups, FF = Forage fish model groups, NUC = Non-upwelling coastal, PED = Pedigree index, [a] = 48 group model, [b] = pre-oil spill model, [c] = post-oil spill model, [d] = ETP7 model, [e] = La Niña model, and [f] = El Niño model.

#	Model name	Model year(s)	Latitude group	Ecosystem type	Model area (km^2)	PED	MG	P	FF	Value data	Krill MG	Citation
1	Western Bering Sea[1]	1980s-90s	High latitude	Arctic	254,000	-	48	22	3	Yes	Yes	(Aydin et al. 2002)
2	Eastern Bering Sea (1)	1980s	High latitude	Arctic	484,508	-	25	14	1	Yes	No	(Trites et al. 1999)
3	Eastern Bering Sea (2)	1980s-90s	High latitude	Arctic	485,000	-	38	19	2	Yes	No	(Aydin et al. 2002)
4	Prince William Sound, Alaska (1)[2]	1980-89	High latitude	Arctic	8,800	0.351	19	6	2	Yes	No	(Dalsgaard & Pauly 1997)
5	Prince William Sound, Alaska (2)[3]	1994-96	High latitude	Arctic	9000	0.675	48	20	5	Yes	No	(Okey & Pauly 1999)
6	Hecate Strait, N. British Columbia	2000	High latitude	NUC	70,000	-	50	34	5	Yes	Yes	(Ainsworth et al. 2002)
7	N. California Current	1990	Upwelling	Upwelling	69,176	-	63	38	3	Yes	Yes	(Field et al. 2006)
8	Gulf of California	1978-79	Tropical/Subtropical	Semi-enclosed	27,900	-	25	8	1	Yes	No	(Arreguín-Sánchez et al. 2002)
9	Huizachi-Caimanero lagoon complex, Mexico	1970-2000	Tropical/Subtropical	Tropical lagoon	175	0.750	26	6	1	Yes	No	(Zetina-Rejón et al. 2003)
10	Golfo de Nicoya, Costa Rica	1980s-90s	Tropical/Subtropical	Tropical lagoon	1,530	-	20	10	1	Yes	No	(Wolff et al. 1998)

11	Golfo Dulce, Costa Rica	1960-90s	Tropical/Subtropical	Tropical lagoon	750	-	20	9	1	No	No	(Wolff et al. 1996)
12	E. Subtropical Pacific Ocean[4]	1993-97	Tropical/Subtropical	Open ocean	32,800,000	-	40	31	2	Yes	No	(Olson & Watters 2003)
13	N. Humboldt Current[5]	1995-96	Upwelling	Upwelling	165,000	0.638	32	15	3	Yes	No	(Tam et al. 2008)
14	N. Humboldt Current[6]	1997-98	Upwelling	Upwelling	165,000	0.638	32	16	3	Yes	No	(Tam et al. 2008)
15	Sechura Bay, Peru	1996	Upwelling	Upwelling	400	0.462	22	5	1	Yes	No	(Taylor et al. 2008)
16	Central Chile	1998	Upwelling	Upwelling	50,042	-	21	8	5	Yes	Yes	(Neira et al. 2004)
17	Tongoy Bay, Chile	1980s-90s	Upwelling	Upwelling	60	-	17	5	1	No	No	(Wolff 1994)
18	Falkland Islands	1990s	Temperate	NUC	527,000	-	44	32	2	Yes	Yes	(Cheung & Pitcher 2005)
19	S. Brazil Bight	1998-99	Tropical/Subtropical	NUC	97,000	-	25	6	2	Yes	No	(Gasalla & Rossi-Wongtschowski 2004)
20	Caeté Estuary, Brazil	1999	Tropical/Subtropical	NUC	220	-	18	4	1	Yes	No	(Wolff et al. 2000)
21	Gulf of Paria	1980s-90s	Tropical/Subtropical	Tropical lagoon	7,600	-	23	11	1	No	No	(Manickchand-Heileman et al. 2004)
22	NE Venezuela shelf	1970s-80s	Tropical/Subtropical	NUC	30,000	-	16	10	1	Yes	No	(Mendoza 1993)
23	Gulf of Salamanca	1997	Tropical/Subtropical	Tropical lagoon	955	0.743	18	6	1	Yes	No	(Duarte & García 2004)
24	Celestun lagoon, Mexico	2001	Tropical/Subtropical	Tropical	28	0.362	19	1	2	Yes	No	(Vega-Cendejas &

				lagoon								Arreguín-Sánchez 2001)
25	Terminos lagoon, Mexico	1980s-90s	Tropical/Subtropical	Tropical lagoon	2,500	-	20	5	1	No	No	(Manickchand-Heileman et al. 1998a)
26	Southwestern Gulf of Mexico	1980s-90s	Tropical/Subtropical	Tropical lagoon	65,000	-	19	9	1	No	No	(Manickchand-Heileman et al. 1998b)
27	Laguna Alvarado, Mexico	1991-94	Tropical/Subtropical	Tropical lagoon	62	0.500	30	9	2	Yes	No	(Cruz-Escalona et al. 2007)
28	Tampamachoco lagoon, Mexico	1980s-90s	Tropical/Subtropical	Tropical lagoon	15	-	23	6	1	No	No	(Rosado-Solórzano & Guzmán del Próo 1998)
29	Gulf of Mexico	1950-2004	Tropical/Subtropical	NUC	1,530,387	-	61	23	6	No	No	(Walters et al. 2008)
30	West Florida shelf	1980s-90s	Tropical/Subtropical	NUC	170,000	-	59	18	2	No	No	(Okey et al. 2004)
31	Chesapeake Bay	2000	Temperate	NUC	10,000	0.450	45	17	5	Yes	No	(Christensen et al. 2009)
32	Gulf of Maine	1977-86	Temperate	NUC	90,700	-	30	12	2	Yes	No	(Heymans 2001)
33	N. Gulf of St. Lawrence	1985-87	Temperate	NUC	103,812	0.651	31	19	3	Yes	No	(Morissette et al. 2003)
34	Newfoundland	1995	Temperate	NUC	495,000	0.396	50	30	4	Yes	No	(Heymans & Pitcher 2002)

35	Lancaster Sound region, Canada	1980s	High latitude	Arctic	97,698	-	32	2	1	No	No	(Mohammed 2001)
36	West Greenland	1991-92	High latitude	Arctic	63,500	0.439	12	4	1	Yes	No	(Pedersen 1994)
37	Icelandic shelf	1997	High latitude	Arctic	115,000	0.295	21	10	2	No	No	(Mendy 1999)
38	Barents Sea (1)	1990	High latitude	Arctic	1,400,000	-	41	18	5	Yes	No	(Blanchard et al. 2002)
39	Barents Sea (2)	1995	High latitude	Arctic	1,400,000	-	41	18	5	Yes	No	(Blanchard et al. 2002)
40	Baltic Sea	1974-2000	Temperate	Semi-enclosed	396,838	-	16	5	4	Yes	No	(Harvey et al. 2003)
41	North Sea	1981	Temperate	NUC	570,000	-	25	8	4	Yes	Yes	(Christensen 1995)
42	English Channel	1995	Temperate	NUC	89,607	-	48	15	4	Yes	No	(Stanford & Pitcher 2004)
43	W. English Channel	1994	Temperate	NUC	56,452	-	52	20	4	Yes	No	(Araújo et al. 2005)
44	Bay of Mont St. Michel, France	2003	Temperate	NUC	250	-	19	1	1	Yes	No	(Arbach Leloup et al. 2008)
45	Cantabrian Sea shelf	1994	Temperate	NUC	16,000	0.669	28	9	2	Yes	No	(Sánchez & Olaso 2004)
46	Azores Archipelago	1997	Temperate	NUC	584,000	0.409	44	15	1	Yes	No	(Guénette & Morato 2001)
47	NW Mediterranean Sea	1994	Temperate	Semi-	4,500	-	23	10	3	Yes	No	(Coll et al. 2006)

				enclosed								
48	Orbetello lagoon, Italy	1996	Temperate	NUC	27	-	9	4	1	Yes	No	(Brando et al. 2004)
49	N. & C. Adriatic Sea	1990s	Temperate	Semi-enclosed	55,500	0.657	40	16	3	Yes	No	(Coll et al. 2007)
50	Black Sea	1989-91	Temperate	Semi-enclosed	423,000	-	11	4	1	Yes	No	(Örek 2000)
51	Atlantic coast of Morocco	1984	Upwelling	Upwelling	586,900	0.382	38	19	2	Yes	No	(Stanford et al. 2004)
52	Banc d'Arguin, Mauritanie	1988-98	Tropical/Subtropical	NUC	10,000	0.537	22	7	1	Yes	No	(Sidi & Diop 2004)
53	Cape Verde Archipelago	1981-85	Tropical/Subtropical	NUC	5,394	-	31	9	1	Yes	No	(Stobberup et al. 2004)
54	Central Atlantic Ocean	1997-98	Temperate	Open ocean	18,419,191	-	39	14	1	Yes	No	(Vasconcellos & Watson 2004)
55	Gambian continental shelf	1995	Tropical/Subtropical	NUC	4,000	-	23	7	2	No	No	(Mendy 2004)
56	Guinea-Bissau continental shelf	1990-92	Tropical/Subtropical	NUC	40,816	-	32	12	2	Yes	No	(Amorim et al. 2004)
57	Senegambia	1990	Tropical/Subtropical	NUC	27,600	-	18	7	2	Yes	No	(Samb & Mendy 2004)
58	Guinean continental shelf	2005	Tropical/Subtropical	NUC	42,969	-	35	21	2	Yes	No	(Gascuel et al. 2009)

59	S. Benguela Current	1990	Upwelling	Upwelling	220,000	-	32	15	4	Yes	No	(Shannon et al. 2003)
60	S. Orkneys/S. Georgia	1990s	High latitude	Antarctic	1,880,000	-	30	22	2	Yes	Yes	(Bredesen 2004)
61	Antarctic Peninsula	1991-2001	High latitude	Antarctic	3,400	-	39	20	2	Yes	Yes	(Erfan & Pitcher 2005)
62	Kerguelen Archipelago EEZ	1987-88	Temperate	NUC	575,100	-	23	15	2	Yes	Yes	(Pruvost et al. 2005)
63	Maputo Bay, Mozambique	1980s-90s	Tropical/Subtropical	NUC	1,100	-	10	4	1	Yes	No	(Paula e Silva et al. 1993)
64	Great Barrier Reef, Australia	2000	Tropical/Subtropical	Tropical lagoon	325,848	-	30	12	2	No	No	(Gribble 2005)
65	Darwin Harbour, Australia	1990-2000	Tropical/Subtropical	NUC	250	0.375	21	5	1	No	No	(Martin 2005)
66	Brunei Darussalam	1989-90	Tropical/Subtropical	Tropical lagoon	7,396	-	13	4	1	Yes	No	(Silvestre et al. 1993)
67	Terengganu, Malaysia	1980s	Tropical/Subtropical	Tropical lagoon	1,050	-	13	2	2	Yes	No	(Liew & Chan 1987)
68	Hong Kong, China	1990s	Tropical/Subtropical	NUC	1,680	-	37	12	1	No	No	(Buchary et al. 2002)
69	Tapong Bay, Taiwan	1999-2001	Tropical/Subtropical	Tropical lagoon	4	0.820	18	1	2	No	No	(Lin et al. 2006)
70	East China Sea	1997-2000	Tropical/Subtropical	Open ocean	770,000	0.636	45	19	6	Yes	No	(Jiang et al. 2008)

71	Bohai Sea	1982-83	Temperate	NUC	77,000	-	13	5	1	Yes	No	(Tong et al. 2000)
72	Central N. Pacific	1990s	Tropical/Subtropical	Open ocean	9,888,350	-	25	20	2	No	No	(Cox et al. 2002)

Table 2.2 Complete Economic Exclusive Zone and High Seas Area (EEZ/HSA) inventory for global extrapolation analysis. EM = Ecopath model, NN = Nearest-Neighbor, LGM = Latitude group mean from Table 2.6, FP = Footprint (% area), IFA = Inshore fishing area, TFCV = Total fisheries catch value (excluding non-cephalopod, non-krill invertebrates), FFCV = Forage fish catch value. HL = High latitude, TM = Temperate, and TS = Tropical-subtropical.

#	EEZ/HSA Name	Estimate type	# of EMs	EM(s)	EM area (km^2)	EEZ/HSA area (km^2)	FP on EEZ/HSA (%)	IFA (km^2)	FP on IFA (%)	TFCV (2006 USD)	FFCV (2006 USD)
1	Alaska (USA)	EM	4	2,3,4,5	494,000	3,770,021	13.1	512,831	96.3	1,182,289,771	12,526,442
2	Albania	EM	1	49	55,500	11,138	100.0	5,297	100.0	3,540,888	55,988
3	Algeria	NN	1	47	-	128,865	-	10,263	-	29,979,780	11,313,000
4	American Samoa	LGM	-	TS	-	404,391	-	437	-	4,986,343	0
5	Andaman & Nicobar Isl. (India)	LGM	-	TS	-	659,912	-	27,648	-	56,611,506	6,351,468
6	Angola	NN	1	59	-	501,050	-	35,363	-	136,531,289	4,151,674
7	Anguilla (UK)	NN	1	22	-	92,178	-	1,600	-	468,998	0
8	Antigua & Barbuda	NN	1	22	-	107,914	-	3,144	-	3,540,761	0
9	Argentina	NN	1	19	-	1,084,386	-	166,486	-	609,270,732	1,930,260
10	Ascension Isl. (St Helena)	LGM	-	TS	-	441,658	-	94	-	1,201,492	0
11	Australia	LGM	-	TS	-	6,362,934	-	978,016	-	633,549,116	0
12	Australia (Christmas Isl.)	LGM	-	TS	-	277,345	-	161	-	5,074,003	441,370
13	Azores Isl. (Portugal)	EM	1	46	584,000	1,056,156	55.3	3,161	100.0	16,582,750	21,534
14	Bahamas	LGM	-	TS	-	629,293	-	62,227	-	2,055,043	0
15	Bahrain	LGM	-	TS	-	8,884	-	6,721	-	31,703,081	757,609
16	Bangladesh	LGM	-	TS	-	78,538	-	31,145	-	226,865,316	65,963,119
17	Barbados	LGM	-	TS	-	186,107	-	320	-	310,195	102,482
18	Belgium	EM	1	42	89,607	3,453	100.0	2,637	100.0	3,341,701	295,740
19	Belize	LGM	-	TS	-	35,995	-	11,808	-	10,255	0

20	Benin	LGM	-	TS	-	30,024	-	1,899	-	3,709,496	331,880
21	Bermuda (UK)	LGM	-	TS	-	450,370	-	699	-	204,301	0
22	Bonaire (Leeward Netherlands Antilles)	LGM	-	TS	-	68,783	-	2,886	-	294,457	0
23	Bosnia & Herzegovina	EM	1	49	55,500	14	100.0	14	100.0	820,486	104,789
24	Bouvet Isl. (Norway)	LGM	-	HL	-	441,163	-	123	-	0	0
25	Brazil	EM	1	19	97,000	3,179,693	3.1	376,117	25.8	856,553,170	98,330,674
26	Brit. Indian Ocean Terr. (UK)	LGM	-	TS	-	638,568	-	10,835	-	1,404,908	0
27	British Virgin Isl. (UK)	LGM	-	TS	-	80,117	-	2,387	-	2,748,226	0
28	Brunei Darussalam	EM	1	66	7,396	25,427	29.1	6,438	100.0	1,213,582	0
29	Bulgaria	EM	1	50	423,000	35,156	100.0	9,334	100.0	145,594	78,173
30	Cambodia	NN	1	67	-	47,827	-	22,431	-	30,968,416	0
31	Cameroon	NN	1	58	-	14,693	-	9,771	-	73,472,999	52,010,267
32	Canada	EM	3	6,33,34	668,812	6,006,154	11.1	1,901,344	35.2	423,796,222	38,106,273
33	Canary Isl. (Spain)	EM	1	51	586,900	455,397	100.0	7,230	100.0	88,822,689	3,882,833
34	Cape Verde	EM	1	53	5,394	796,840	0.7	5,697	94.7	5,517,524	0
35	Cayman Isl. (UK)	LGM	-	TS	-	119,137	-	649	-	91,658	0
36	Channel Isl. (UK)	EM	2	42,43	89,607	11,658	100.0	9,148	100.0	20,599,923	511,024
37	Chile	EM	1	16	50,042	2,009,299	2.5	211,070	23.7	1,348,903,463	95,624,889
38	China	EM	2	70,71	847,000	2,285,872	37.1	358,425	100.0	6,013,317,218	598,024,991
39	Clipperton Isl. (France)	LGM	-	TS	-	431,263	-	2	-	2,349,083	0
40	Cocos (Keeling) Isl. (Australia)	LGM	-	TS	-	467,249	-	178	-	6,196,878	454,711
41	Colombia	EM	1	23	955	817,816	0.1	39,460	2.4	22,264,802	802,950
42	Comoros Isl.	EM	1	63	1,100	164,691	0.7	1,553	70.8	5,576,537	113,957
43	Congo (ex-Zaire)	NN	1	59	-	1,072	-	1,088	-	1,861,882	192,015
44	Congo, R. of	NN	1	59	-	40,499	-	7,044	-	13,571,427	3,118,168

45	Cook Isl. (New Zealand)	LGM	-	TS	-	1,960,135	-	479	-	2,998,062	0
46	Costa Rica	EM	1	10	1,530	572,014	0.3	15,371	10.0	2,481,033	87,084
47	Côte d'Ivoire	NN	1	58	-	174,545	-	8,332	-	16,925,631	1,006,418
48	Croatia	EM	1	49	55,500	56,374	98.4	38,763	100.0	113,993,584	18,586,310
49	Crozet Isl. (France)	LGM	-	TM	-	574,558	-	5,471	-	1,612,735	0
50	Cuba	LGM	-	TS	-	365,448	-	59,411	-	20,182,139	748,327
51	Cyprus	NN	1	49	-	98,550	-	3,343	-	25,904,360	349,695
52	Denmark	EM	1	41	570,000	107,579	100.0	57,838	100.0	246,543,973	37,867,771
53	Desventuradas Isl. (Chile)	EM	1	16	50,042	449,805	11.1	265	100.0	60,605,096	0
54	Djibouti	LGM	-	TS	-	6,947	-	2,525	-	184,728	0
55	Dominica	LGM	-	TS	-	28,626	-	606	-	3,725,891	536,452
56	Dominican Republic	LGM	-	TS	-	269,285	-	7,274	-	18,136,006	45,921
57	Easter Isl. (Chile)	LGM	-	TS	-	720,395	-	269	-	17,053,581	0
58	Ecuador	NN	2	13,14	-	236,597	-	23,894	-	39,348,331	7,655,604
59	Egypt	NN	1	49	-	261,824	-	58,027	-	13,340,647	418,327
60	El Salvador	NN	1	10	-	93,761	-	12,856	-	7,331,895	0
61	Equatorial Guinea	NN	1	59	-	308,337	-	7,544	-	889,433	0
62	Eritrea	LGM	-	TS	-	78,703	-	55,493	-	5,820,206	30,411
63	Estonia	EM	1	40	396,838	39,940	100.0	28,217	100.0	23,486,102	21,236,615
64	Faeroe Isl. (Denmark)	EM	1	41	570,000	269,866	100.0	13,656	100.0	382,849,370	15,803,866
65	Falkland Isl. (UK)	EM	1	18	527,000	550,872	95.7	43,836	100.0	49,419,203	15
66	Fiji	LGM	-	TS	-	1,281,122	-	49,424	-	58,006,951	42,546
67	Finland	EM	1	40	396,838	90,828	100.0	58,137	100.0	52,881,129	42,142,810
68	France	EM	3	42,43,47	94,107	334,604	28.1	85,367	100.0	406,391,189	16,758,926
69	French Guiana	NN	1	20	-	133,949	-	16,238	-	5,517,128	0
70	French Polynesia	LGM	-	TS	-	4,767,242	-	10,767	-	32,300,110	0
71	Gabon	NN	1	59	-	193,627	-	27,154	-	35,611,003	13,049,930

72	Galapagos Isl. (Ecuador)	NN	2	13,14	-	835,936	-	11,424	-	33,250,996	571,297
73	Gambia	EM	1	57	27,600	22,630	100.0	4,065	100.0	27,333,200	16,542,816
74	Gaza Strip	NN	1	49	-	2,584	-	905	-	3,221,314	414,856
75	Georgia	EM	1	50	423,000	22,765	100.0	1,536	100.0	41,467	28,165
76	Germany	EM	2	40,41	966,838	57,259	100.0	29,918	100.0	47,387,822	5,103,776
77	Ghana	NN	1	59	-	224,908	-	16,699	-	81,060,814	15,623,747
78	Gibraltar (UK)	NN	1	47	-	426	-	58	-	237	0
79	Greece	EM	1	49	55,500	494,605	11.2	178,060	31.2	554,039,728	55,667,128
80	Greenland	EM	1	36	63,500	2,353,703	2.7	384,853	16.5	307,068,748	4,359,916
81	Grenada	LGM	-	TS	-	26,158	-	943	-	1,831,788	213
82	Guadeloupe (France)	LGM	-	TS	-	95,978	-	4,653	-	25,461,610	0
83	Guam (USA)	LGM	-	TS	-	221,504	-	339	-	6,505,470	0
84	Guatemala	NN	1	10	-	117,743	-	12,618	-	19,826	0
85	Guinea	NN	1	58	-	109,456	-	17,761	-	111,457,039	41,485,737
86	Guinea-Bissau	EM	1	56	40,816	106,117	38.5	24,440	100.0	18,426,456	0
87	Guyana	NN	1	22	-	135,900	-	22,695	-	62,080,218	0
88	Haiti	LGM	-	TS	-	112,025	-	7,081	-	15,198,528	0
89	Hawaii Main Islands (USA)	LGM	-	TS	-	895,346	-	7,720	-	10,015,762	0
90	Hawaii Northwest Islands (USA)	LGM	-	TS	-	1,579,538	-	4,784	-	9,681,503	0
91	Heard & McDonald Isl. (Australia)	LGM	-	TM	-	417,015	-	2,787	-	33,157,232	0
92	High seas - Arctic Sea	LGM	-	HL	-	2,532,446	-	-	-	24,234	0
93	High seas - Atlantic, Antarctic	EM	1	61	3,400	10,346,850	0.0	-	-	134,160,208	128,785,320
94	High seas - Atlantic, Eastern Central	EM	1	54	18,419,191	8,981,189	100.0	-	-	408,298,617	544,489
95	High seas - Atlantic,	NN	1	54	-	5,435,509	-	-	-	324,521,967	2,053,281

	Northeast										
96	High seas - Atlantic, Northwest	NN	1	54	-	2,637,160	-	-	-	100,663,511	6,412,582
97	High seas - Atlantic, Southeast	NN	1	54	-	14,958,561	-	-	-	214,652,822	9,784
98	High seas - Atlantic, Southwest	NN	1	54	-	12,332,183	-	-	-	1,029,065,004	288,235
99	High seas - Atlantic, Western Central	NN	1	54	-	7,334,480	-	-	-	193,703,489	239,353
100	High seas - Indian Ocean, Antarctic	LGM	-	TS	-	10,876,795	-	-	-	2,658,658	0
101	High seas - Indian Ocean, Eastern	LGM	-	TS	-	22,176,590	-	-	-	1,165,267,773	23,885,374
102	High seas - Indian Ocean, Western	LGM	-	TS	-	17,027,045	-	-	-	2,022,598,776	315,849
103	High seas - Pacific, Antarctic	NN	1	61	-	9,997,724	-	-	-	3,129,326	0
104	High seas - Pacific, Eastern Central	EM	1	12	32,800,000	30,435,357	100.0	-	-	1,624,622,942	89,010
105	High seas - Pacific, Northeast	NN	1	12	-	4,585,150	-	-	-	63,147,853	5,364,250
106	High seas - Pacific, Northwest	NN	1	12	-	10,308,701	-	-	-	1,942,710,022	18,788,440
107	High seas - Pacific, Southeast	EM	1	12	32,800,000	24,696,759	100.0	-	-	1,297,774,567	290,496
108	High seas - Pacific, Southwest	NN	1	12	-	20,188,772	-	-	-	492,602,939	0
109	High seas - Pacific, Western Central	NN	1	12	-	6,378,477	-	-	-	5,368,243,275	1,369,692
110	Honduras	LGM	-	TS	-	240,240	-	24,300	-	3,259,696	0
111	Hong Kong	NN	1	67	-	2,097	-	2,084	-	52,801,236	1,688,895
112	Howland & Baker Isl. (USA)	LGM	-	TS	-	434,921	-	0	-	2,532,597	0
113	Iceland	NN	1	41	-	772,218	-	67,303	-	944,369,181	33,128,711

114	India (mainland)	LGM	-	TS	-	1,630,356	-	207,278	-	1,747,262,030	340,593,924
115	Indonesia (Eastern)	LGM	-	TS	-	3,617,349	-	512,980	-	881,388,037	89,460,133
116	Indonesia (Western)	LGM	-	TS	-	2,462,028	-	576,211	-	631,463,869	56,435,488
117	Iran	LGM	-	TS	-	164,051	-	80,305	-	478,184,183	9,905,709
118	Iraq	LGM	-	TS	-	597	-	597	-	729,074	6,840
119	Ireland	NN	2	42,43	-	410,534	-	58,678	-	501,322,581	4,912,933
120	Israel	NN	1	49	-	27,346	-	3,196	-	11,393,177	200,474
121	Italy	EM	2	48,49	55,527	537,932	10.3	94,054	100.0	285,614,722	21,629,289
122	J. Fernandez, Felix and Ambrosio Isl. (Chile)	NN	1	16	-	502,490	-	283	-	68,717,296	49,280
123	Jamaica	LGM	-	TS	-	263,283	-	4,512	-	18,499,349	0
124	Jan Mayen Isl. (Norway)	LGM	-	HL	-	292,567	-	1,615	-	37,846,309	21,946
125	Japan (main islands)	NN	1	70	-	1,843,270	-	224,481	-	5,238,184,599	458,890,839
126	Japan (outer islands)	NN	1	70	-	2,625,750	-	35,152	-	3,756,404,871	328,258,376
127	Jarvis Isl. (USA)	LGM	-	TS	-	316,665	-	0	-	2,531,162	0
128	Johnston Atoll (USA)	LGM	-	TS	-	442,635	-	136	-	2,852,588	0
129	Jordan	LGM	-	TS	-	95	-	27	-	291,032	26
130	Kenya	NN	1	63	-	111,999	-	8,759	-	1,751,708	0
131	Kerguelen Isl. (France)	EM	1	62	575,100	567,732	100.0	27,254	100.0	12,719,392	0
132	Kiribati	LGM	-	TS	-	3,437,345	-	6,550	-	64,820,095	217,050
133	Korea (North)	NN	1	71	-	115,649	-	30,115	-	155,035,107	0
134	Korea (South)	NN	1	71	-	475,469	-	97,246	-	679,802,698	80,490,506
135	Kuwait	LGM	-	TS	-	12,236	-	10,297	-	17,592,399	173,899
136	Latvia	EM	1	40	396,838	32,021	100.0	14,186	100.0	32,290,978	27,144,993
137	Lebanon	NN	1	49	-	19,196	-	526	-	15,246,526	165,788

138	Liberia	NN	1	58	-	246,152	-	14,176	-	9,385,742	172,366
139	Libya	NN	1	47	-	355,120	-	50,980	-	8,226,116	405,067
140	Lithuania	EM	1	40	396,838	6,104	100.0	2,758	100.0	9,541,067	7,488,829
141	Lord Howe Isl. (Australia)	LGM	-	TS	-	543,346	-	461	-	19,712,433	0
142	Macau (China)	LGM	-	TS	-	41	-	41	-	15,312,299	1,699,864
143	Macquarie Isl. (Australia)	LGM	-	TM	-	475,847	-	256	-	4,191,045	0
144	Madagascar	NN	1	63	-	1,198,722	-	83,191	-	160,792,045	0
145	Madeira Isl. (Portugal)	NN	1	45	-	454,495	-	901	-	11,206,097	500,030
146	Malaysia (Peninsula East)	EM	1	67	1,050	132,973	0.8	47,540	2.2	419,888,077	22,335,687
147	Malaysia (Peninsula West)	EM	1	67	1,050	68,747	1.5	37,658	2.8	448,598,226	50,947,897
148	Malaysia (Sabah)	NN	1	66	-	89,618	-	47,678	-	244,551,677	16,352,252
149	Malaysia (Sarawak)	NN	1	66	-	155,938	-	36,476	-	384,215,771	22,659,848
150	Maldives	LGM	-	TS	-	916,189	-	32,700	-	766,673,644	0
151	Malta	NN	1	49	-	55,556	-	2,384	-	29,767,467	1,161,691
152	Marshall Isl.	LGM	-	TS	-	1,992,232	-	14,885	-	92,168,789	0
153	Martinique (France)	NN	1	47	-	47,640	-	1,576	-	2,962,539	898,563
154	Mauritania	EM	1	52	10,000	155,422	6.4	24,596	40.7	269,254,350	18,233,382
155	Mauritius	LGM	-	TS	-	1,272,787	-	2,222	-	42,672,689	0
156	Mayotte (France)	NN	1	63	-	63,078	-	1,141	-	4,331,852	0
157	Mexico	EM	4	8,9,24,27	28,165	3,269,386	0.9	251,122	11.2	539,137,572	196,738,292
158	Micronesia	LGM	-	TS	-	2,992,597	-	8,293	-	210,257,190	0
159	Monaco	NN	1	47	-	285	-	4	-	390,686	183,730
160	Montenegro	NN	1	47	-	7,415	-	3,508	-	10,092,290	1,002,696
161	Montserrat (UK)	NN	1	47	-	7,582	-	127	-	130,277	0
162	Morocco	EM	1	51	586,900	272,059	100.0	49,033	100.0	355,722,270	41,590,931
163	Mozambique	EM	1	63	1,100	571,955	0.2	73,307	1.5	17,391,171	0

164	Mozambique Channel Isl. (France)	EM	1	63	1,100	352,117	0.3	314	100.0	10,909,449	0
165	Myanmar	LGM	-	TS	-	520,262	-	124,280	-	1,135,482,263	4,912,914
166	Namibia	NN	1	59	-	560,152	-	53,325	-	293,389,079	1,471,554
167	Nauru	LGM	-	TS	-	308,502	-	11	-	17,909,216	0
168	Navassa Isl. (Haiti)	LGM	-	TS	-	11,494	-	22	-	3,300,814	0
169	Netherlands	EM	1	41	570,000	63,912	100.0	19,651	100.0	85,946,592	6,808,915
170	New Caledonia (France)	LGM	-	TS	-	1,422,543	-	28,666	-	628,460	0
171	New Zealand	LGM	-	TS	-	3,423,231	-	193,773	-	674,443,602	1,361,460
172	Nicaragua	LGM	-	TS	-	127,488	-	49,756	-	14,525,680	0
173	Nigeria	NN	1	59	-	216,789	-	32,959	-	167,372,765	35,220,752
174	Niue (New Zealand)	LGM	-	TS	-	316,629	-	144	-	20,771	0
175	Norfolk Isl. (Australia)	LGM	-	TS	-	431,121	-	2,654	-	1,236,510	0
176	Northern Marianas (USA)	LGM	-	TS	-	749,268	-	741	-	11,273,938	0
177	Norway	EM	3	38,39,41	1,970,000	1,395,753	100.0	110,640	100.0	1,270,660,912	202,551,925
178	Oman	LGM	-	TS	-	535,912	-	51,403	-	279,137,276	27,365,531
179	Pakistan	LGM	-	TS	-	221,435	-	30,958	-	347,498,144	38,581,344
180	Palau	LGM	-	TS	-	604,289	-	1,989	-	45,562,103	0
181	Palmyra Atoll & Kingman Reef (USA)	LGM	-	TS	-	352,300	-	943	-	2,739,452	0
182	Panama	NN	1	10	-	331,465	-	46,652	-	51,027,177	30,019,062
183	Papua New Guinea	LGM	-	TS	-	2,396,214	-	170,596	-	2,444,915,887	0
184	Peru	EM	3	13,14,15	165,400	906,454	18.2	55,339	100.0	758,825,963	366,816,781
185	Philippines	LGM	-	TS	-	2,265,684	-	328,592	-	1,594,314,019	221,459,396
186	Pitcairn (UK)	LGM	-	TS	-	836,108	-	78	-	3,693	0
187	Poland	EM	1	40	396,838	31,600	100.0	19,427	100.0	41,887,791	18,604,700

188	Portugal	NN	1	45	-	322,197	-	18,437	-	125,318,096	20,605,422
189	Prince Edward Isl. (South Africa)	NN	1	59	-	473,380	-	832	-	65,079	0
190	Puerto Rico (USA)	LGM	-	TS	-	177,685	-	7,883	-	9,039,856	88,635
191	Qatar	LGM	-	TS	-	31,870	-	23,989	-	21,337,159	0
192	Réunion (France)	LGM	-	TS	-	315,058	-	563	-	4,110,347	0
193	Romania	EM	1	50	423,000	20,598	100.0	8,440	100.0	55,359	19,044
194	Russia (Baltic Sea, Kaliningrad)	EM	1	40	396,838	11,634	100.0	6,929	100.0	20,033,975	11,004,715
195	Russia (Baltic Sea, St. Petersburg)	EM	1	40	396,838	12,759	100.0	11,456	100.0	6,497,214	4,474,465
196	Russia (Barents Sea)	EM	2	38,39	1,400,000	1,308,140	100.0	260,036	100.0	266,332,452	157,160
197	Russia (Black Sea)	EM	1	50	423,000	66,854	100.0	16,360	100.0	11,211,469	2,214,816
198	Russia (Pacific)	EM	1	1	254,000	3,419,202	7.4	411,933	100.0	5,591,103,321	209,925,131
199	Russia (Siberia)	NN	2	38,39	-	3,277,292	-	641,981	-	3,778,027	0
200	Saint Helena (UK)	LGM	-	TS	-	444,916	-	122	-	25,513	0
201	Saint Kitts & Nevis	LGM	-	TS	-	10,201	-	551	-	516,465	0
202	Saint Lucia	LGM	-	TS	-	15,484	-	416	-	3,343,370	17,725
203	Saint Pierre & Miquelon (France)	NN	1	34	-	12,334	-	4,917	-	243,814	0
204	Saint Vincent & the Grenadines	LGM	-	TS	-	36,314	-	2,080	-	357,195	0
205	Samoa	LGM	-	TS	-	131,812	-	2,675	-	209,280	0
206	Sao Tome & Principe	NN	1	59	-	165,364	-	1,499	-	5,926,500	340,031
207	Saudi Arabia (Persian Gulf)	LGM	-	TS	-	34,023	-	28,334	-	126,928,291	5,916,644
208	Saudi Arabia (Red Sea)	LGM	-	TS	-	185,882	-	57,920	-	53,092,953	105,720
209	Senegal	NN	1	52	-	157,550	-	16,943	-	221,614,894	49,112,168
210	Seychelles	NN	1	63	-	1,332,031	-	16,699	-	40,420,903	0
211	Sierra Leone	NN	1	58	-	159,744	-	16,600	-	109,427,753	75,034,089

212	Singapore	NN	1	67	-	823	-	814	-	31,054,919	897,964
213	Slovenia	NN	1	49	-	186	-	185	-	635,560	292,475
214	Solomon Isl.	LGM	-	TS	-	1,597,492	-	55,002	-	119,864,410	0
215	Somalia	LGM	-	TS	-	830,389	-	50,990	-	38,438,367	0
216	South Africa	NN	1	59	-	1,066,655	-	86,916	-	184,533,943	40,930,102
217	South Georgia & Sandwich Isl. (UK)	EM	1	60	1,880,000	1,449,532	100.0	14,950	100.0	3,009,127	0
218	Spain	EM	2	45,47	20,500	551,874	3.7	24,170	100.0	612,216,515	63,186,340
219	Sri Lanka	LGM	-	TS	-	530,684	-	27,193	-	43,102,002	6,914,434
220	St Paul & Amsterdam Isl. (France)	LGM	-	TM	-	509,015	-	151	-	1,771,839	0
221	Sudan	LGM	-	TS	-	88,067	-	24,652	-	22,754,978	41,759
222	Suriname	NN	1	22	-	128,318	-	18,182	-	36,611,199	0
223	Svalbard Isl. (Norway)	NN	2	38,39	-	426,119	-	92,864	-	195,963,556	428,793
224	Sweden	EM	1	40	396,838	170,086	100.0	100,596	100.0	151,718,417	100,512,191
225	Syrian Arab Republic	NN	1	49	-	10,222	-	469	-	5,711,716	305,232
226	Taiwan	NN	1	70	-	1,149,189	-	45,529	-	596,004,172	3,574,650
227	Tanzania	NN	1	63	-	241,541	-	23,557	-	14,520,755	140,914
228	Thailand	NN	1	67	-	306,365	-	122,330	-	266,415,979	12,784,078
229	Timor Leste	LGM	-	TS	-	77,256	-	3,023	-	278,587	0
230	Togo	NN	1	59	-	15,375	-	950	-	3,561,099	1,233,255
231	Tokelau (New Zealand)	LGM	-	TS	-	319,031	-	144	-	188,058	0
232	Tonga	LGM	-	TS	-	664,853	-	8,479	-	655,362	0
233	Trindade & Martin Vaz Isl. (Brazil)	LGM	-	TS	-	468,615	-	11	-	7,648,841	249,059
234	Trinidad & Tobago	NN	1	22	-	77,502	-	18,804	-	5,576,508	0
235	Tristan da Cunha Isl. (St Helena)	LGM	-	TS	-	754,720	-	241	-	1,204,164	0

#	Name										
236	Tromelin Isl. (France)	NN	1	63	-	270,455	-	1	-	7,770,666	0
237	Tunisia	NN	1	47	-	102,362	-	41,389	-	52,450,506	4,070,404
238	Turkey (Black Sea)	EM	1	50	423,000	172,199	100.0	19,608	100.0	233,363,915	76,451,528
239	Turkey (Mediterranean Sea)	NN	1	49	-	83,588	-	33,200	-	342,945,693	142,400,296
240	Turks & Caicos Isl. (UK)	LGM	-	TS	-	154,068	-	9,060	-	1,386	0
241	Tuvalu	LGM	-	TS	-	751,797	-	509	-	17,490,526	0
242	Ukraine	NN	1	50	-	144,038	-	55,044	-	24,631,853	4,439,821
243	United Arab Emirates	LGM	-	TS	-	57,194	-	52,678	-	108,199,620	7,093,430
244	United Kingdom	EM	2	41,43	626,452	773,676	81.0	216,763	100.0	955,754,004	78,972,011
245	United States, East Coast	EM	2	31,32	100,700	915,763	11.0	182,102	55.3	319,408,112	125,278,753
246	United States Gulf of Mexico	LGM	-	TS	-	707,832	-	138,365	-	250,618,158	169,318,390
247	United States, West Coast	EM	1	7	69,176	825,549	8.4	54,109	100.0	203,963,519	10,965,520
248	Uruguay	NN	1	19	-	132,286	-	25,838	-	105,205,883	733,374
249	US Virgin Isl.	LGM	-	TS	-	33,744	-	1,536	-	4,099,453	38,079
250	Vanuatu	LGM	-	TS	-	827,891	-	13,986	-	122,240,949	0
251	Venezuela	NN	1	22	-	471,507	-	109,426	-	156,869,483	9,364,805
252	Viet Nam	NN	1	67	-	1,396,299	-	164,775	-	1,403,764,772	0
253	Wake Isl. (USA)	LGM	-	TS	-	407,241	-	13	-	3,914,679	0
254	Wallis & Futuna Isl. (France)	LGM	-	TS	-	258,269	-	514	-	794,806	0
255	Western Sahara (Morocco)	EM	1	51	586,900	300,653	100.0	39,543	100.0	380,818,639	121,744,480
256	Windward Netherlands Antilles	LGM	-	TS	-	12,169	-	1,609	-	180,298	0
257	Yemen	LGM	-	TS	-	544,416	-	50,216	-	275,781,880	7,881,570

Table 2.3 Summary of Table 2.2 data, including Ecopath model coverage of Economic Exclusive Zones and High Seas Areas (EEZ/HSAs) and inshore fishing areas (IFAs) in terms of area, total fisheries catch value (excluding non-cephalopod, non-krill invertebrates) (TFCV), total forage fish catch value (FFCV) and total support service catch value. (SSCV).

	Number	% of total	Area (km^2)	% of total	TFCV (2006 USD)	% of total	FFCV (2006 USD)	% of total	SSCV (2006 USD)	% of total
EEZ/HSA										
EEZ/HSAs where models represent ≥50% of EEZ/HSA	36	14%	73,559,702	20%	8,246,049,577	11%	862,926,926	15%	1,987,166,610	18%
EEZ/HSAs where models representing <50% of EEZ/HSA	28	11%	45,420,885	12%	20,818,915,746	28%	2,135,245,622	38%	3,493,607,298	31%
EEZ/HSAs with models	64	25%	118,980,587	33%	29,064,965,322	39%	2,998,172,548	53%	5,480,773,909	48%
EEZ/HSAs without models	193	75%	246,554,598	67%	45,095,167,481	61%	2,662,206,598	47%	5,822,757,670	52%
TOTAL EEZ/HSAs	257	100%	365,535,185	100%	74,160,132,803	100%	5,660,379,145	100%	11,303,531,578	100%
IFA										
IFAs where models represent ≥50% of IFA area	48	20%	3,067,454	22%	20,390,732,426	35%	2,287,229,060	42%	3,630,376,589	48%
IFAs where models representing <50% of IFA area	12	5%	3,540,498	25%	5,209,376,563	9%	581,234,172	11%	926,924,820	12%
IFAs with models	60	25%	6,607,952	47%	25,600,108,989	44%	2,868,463,232	52%	4,557,301,409	61%
IFAs without models	179	75%	7,347,259	53%	32,172,177,833	56%	2,603,479,758	48%	2,934,017,206	39%
TOTAL IFAs	239	100%	13,955,211	100%	57,772,286,821	100%	5,471,942,990	100%	7,491,318,616	100%

Table 2.4 Mean Ecopath value ratios (EVR) for all latitude groups. N = number of Ecopath models with value data, SD = standard deviation of EVR latitude values.

Latitude group	N	Mean EVR	SD
High latitude	10	0.188	0.258
Temperate	20	0.196	0.118
Tropical/Subtropical	19	0.101	0.104
Upwelling	7	0.228	0.237
Total	56	0.166	0.166

Table 2.5 Predators with ≥75% forage fish in their diets found in this synthesis that have taxonomic information and are evaluated by the International Union for Conservation of Nature (IUCN) Red List. Model numbers correspond to model names in Table 2.1. MM = marine mammal, SB= seabird, LPF= large predatory bony fish, E= Endangered, LC= Least concern, NT= Near threatened, and V= Vulnerable. [1]IUCN (2013) IUCN Red List of Threatened Species. Version 2013.2 http://www.iucnredlist.org Downloaded on March 2014.

Pred. type	Common name	Scientific name	IUCN[1] status	Population trend	Model (s)
MM	Sei whale	*Balaenoptera borealis*	E	Unknown	1,60
MM	Blue whale	*Balaenoptera musculus*	E	Increasing	1,60
MM	Fin whale	*Balaenoptera physalus*	E	Unknown	1,60
MM	Common Minke whale	*Balaenoptera acutorostrata*	LC	Stable	1,60
MM	Southern Right whale	*Eubalaena australis*	LC	Increasing	60
MM	Grey seal	*Halichoerus grypus*	LC	Increasing	40
MM	Crabeater seal	*Lobodon carcinophagus*	LC	Unknown	60
MM	Humpback whale	*Megaptera novaeangliae*	LC	Increasing	1,60
MM	Ringed seal	*Phoca hispida*	LC	Unknown	40
SB	Black-browed albatross	*Thalassarche melanophrys*	NT	Decreasing	18
SB	Macaroni penguin	*Eudyptes chrysolophus*	V	Decreasing	60,62
SB	Humboldt penguin	*Spheniscus humboldti*	V	Decreasing	17
SB	Peruvian pelican	*Pelecanus thagus*	NT	Increasing	13,14,15,17
SB	Guanay cormorant	*Phalacrocorax bougainvillii*	NT	Decreasing	13,14,15
SB	Sooty Shearwater	*Puffinus griseus*	NT	Decreasing	1
SB	Gentoo penguin	*Pygoscelis papua*	NT	Decreasing	60,62
SB	King penguin	*Aptenodytes patagonicus*	LC	Increasing	62
SB	Rhinoceros Auklet	*Cerorhinca monocerata*	LC	Decreasing	1
SB	Southern Rockhopper penguin	*Eudyptes chrysocome*	V	Decreasing	62
SB	Tufted puffin	*Fratercula cirrhata*	LC	Decreasing	1
SB	Southern Giant-petrel	*Macronectes giganteus*	LC	Increasing	18
SB	Cassin's auklet	*Ptychoramphus aleuticus*	LC	Decreasing	1
SB	Peruvian booby	*Sula variegata*	LC	Stable	13,14,15,17
SB	Common guillemot	*Uria aalge*	LC	Increasing	1
LPF	Yellowfin tuna	*Thunnus albacares*	NT	Decreasing	13,14,56
LPF	Common dolphinfish	*Coryphaena hippurus*	LC	Stable	13,14
LPF	West African ladyfish	*Elops lacerta*	LC	Unknown	56
LPF	Skipjack tuna	*Katsuwonus pelamis*	LC	Stable	56
LPF	North Pacific hake	*Merluccius productus*	LC	Unknown	7
LPF	Sockeye salmon	*Oncorhynchus nerka*	LC	Stable	4,5
LPF	Pacific bonito	*Sarda chiliensis*	LC	Decreasing	13,14

Table 2.6 Ecopath value ratios (EVR) for all 56 Ecopath models with value data. Model number corresponds to models in Table 2.1.

Model no.	EVR	Model no.	EVR
1	0.299	39	0.405
2	0.019	40	0.308
3	0.024	41	0.206
4	0.808	42	0.061
5	0.002	43	0.086
6	0.316	44	0.300
7	0.655	45	0.050
8	0.202	46	0.423
9	0.026	47	0.220
10	0.031	48	0.019
12	0.296	49	0.118
13	0.158	50	0.399
14	0.096	51	0.115
15	0.007	52	0.023
16	0.461	53	0.313
18	0.271	54	0.128
19	0.011	56	0.080
20	0.106	57	0.031
22	0.326	58	0.056
23	0.084	59	0.102
24	0.010	60	0.072
27	0.045	61	0.050
31	0.250	62	0.249
32	0.059	63	0.079
33	0.191	66	0.106
34	0.174	67	0.032
36	0.012	70	0.067
38	0.405	71	0.097

Chapter 3. Characteristics of forage fish predators and fisheries

3.1 Introduction

Forage fish (i.e. small schooling pelagic fish and euphausiids) are among the most ecologically and economically important species in marine ecosystems (Cury et al. 2000, Bakun et al. 2010, Smith et al. 2011, Pikitch et al. 2012, Pikitch et al. 2014). These species not only represent some of the largest fisheries in the world (FAO 2012), but they are critical to maintaining healthy marine ecosystems, largely by transferring energy derived from low trophic levels (i.e. planktonic organisms) to upper trophic level predators (i.e. seabirds, marine mammals, and predatory fish) (Cury et al. 2000, Bakun et al. 2010, Pikitch et al. 2012). As such, fluctuations in their biomass can oftentimes have far reaching ecosystem impacts (Cury et al. 2000, Fréon et al. 2005, Bakun et al. 2010, Smith et al. 2011, Roux et al. 2013).

The sustainable exploitation of forage fish species globally has received significant attention and increased urgency in recent years (Pikitch et al. 2004, Cury et al. 2011, Smith et al. 2011, Pikitch et al. 2012). Mounting evidence of the perils of managing forage fish species in a single-species framework has led to increased interest and calls for a more holistic, ecosystem-based approach to their management (Pikitch et al. 2004, Beddington et al. 2007, Richerson et al. 2010, Pinsky et al. 2011, Pikitch 2012, Pikitch et al. 2012), especially as demand for human uses continues to rise (Tacon & Metian 2013). Ecosystem-based fisheries management (EBFM) is not without its uncertainties and generally requires substantial information about abiotic factors, ecosystem dynamics and potential trade-offs (Brodziak & Link 2002, Pikitch et al. 2004, Link 2010, Pikitch et al. 2012, Essington & Plagányi 2013). Implementation of EBFM, however, is not exclusive to well-studied ecosystems, as promising frameworks, precautionary principles, guidelines and methods exist to inform management in fished ecosystems that are currently data limited or deficient (Tallis et al. 2010, Pikitch et al. 2012, Carey et al. 2013, Essington & Plagányi 2013, Pikitch et al. 2014).

One particularly crucial aspect for EBFM of forage species is an understanding of the importance and relative contributions these species make to marine predators (Pikitch et al. 2004,

Pikitch et al. 2012, Essington & Plagányi 2013). Syntheses of diet data for forage fish predators (e.g. Pikitch et al. 2014) can be especially useful in this regard, as they can elucidate trends across ecosystems and latitudes. For instance, it is quite common for marine ecosystems to have at least one predator which relies on forage fish for 50% or more of its dietary needs, and almost a certainty to find such a predator in upwelling and Antarctic ecosystems (Pikitch et al. 2014). Detailed dietary data can therefore help scientists and managers screen for potential predators that may be sensitive to fluctuations in forage fish biomass.

Recently, Pikitch et al. (2012) demonstrated that impacts to forage fish predators from forage fisheries can be estimated solely on the dietary information of predators using the "PREP" equation. This approach could be especially useful to managers that are trying to assess the possible impacts of forage fisheries to marine predators, but lack the data necessary to create their own ecosystem models to examine these questions directly (Pikitch et al. 2012). As our oceans and coastal areas have already experienced dramatic declines in the abundance of many of these upper trophic level predators (Jackson et al. 2001, Lotze et al. 2006, Lotze & Worm 2009, Hoffmann et al. 2010), it is vital that predators are accounted for in forage fishery management schemes, regardless of data deficiencies.

In addition, fisheries can impact marine ecosystems in a variety of ways that are not always apparent and straightforward (Jennings & Kaiser 1998, Worm et al. 2006, Coll et al. 2008, Richardson et al. 2009, Engelhard et al. 2014). Elucidating the direct and indirect interactions between fisheries and marine predators has been of great interest to fisheries managers and scientists globally, particularly for seabirds (Tasker et al. 2000, Furness 2003, Wagner & Boersma 2011) and marine mammals (DeMaster et al. 2001, Plagányi & Butterworth 2005, Bearzi et al. 2006, Read et al. 2006, Read 2008). However, only a few studies have evaluated the potential for resource overlap and competition between these predators and fisheries globally (Kaschner & Pauly 2004, Kaschner et al. 2006, Karpouzi et al. 2007).

This study synthesized forage fish predator data from a variety of fished food web models (i.e. Ecopath) across the world and calculated a variety of ecological indices, with the aim of informing managers and scientists in ecosystems with limited data on these taxonomic groups. Three factors were specifically investigated: 1) the relative importance of forage fish species to

the diets and production of seabirds, marine mammals and large predatory fish, 2) a determination of the preferred prey (Chesson 1983) and the degree of trophic specialization (Christensen & Pauly 1992, Pauly et al. 2000, Christensen et al. 2008) found amongst these predator groups, and 3) an evaluation of ecosystems where these predators (Morissette et al. 2012) and fisheries (Christensen & Pauly 1992, Pauly et al. 2000, Christensen et al. 2008) may be competing for similar prey and to what extent this occurs (Kaschner & Pauly 2004). These factors were evaluated based on known latitudinal trends previously revealed in Chapter 2 (Pikitch et al. 2014). The potential utility of this study and approach is discussed in the context of advancing forage fish predator information for EBFM in data poor regions.

3.2 Materials and Methods
3.2.1 Synthesis of Ecopath models

Data from a total of 43 Ecopath models representing fished marine ecosystems across the world were obtained for this study (Figure 3.1). Forty one of the models were obtained from an existing database (Pikitch et al. 2014) and two were obtained from publications (Northern Gulf of Mexico (Geers 2012) and Delaware Bay (Frisk et al. 2011)) (Table 3.1). All models met the requirements established in Pikitch et al. (2014), with the additional requirement that these models included at least one species from each of the major predator groups (i.e. seabirds, marine mammals, and large predatory bony fish (i.e. >90 cm maximum total length). Sharks were excluded from the large predatory fish group, as they were not present in all ecosystem models and when present, were often grouped with other elasmobranchs with different trophic habits (i.e. batoids and chimeras). In this study, forage fish were defined according to Pikitch et al. (2014), which included krill as a forage species, but not cephalopods, shrimps, or fish which do not fulfill this role as adults (e.g. North Pacific hake, Blue whiting, etc.).

Most models represented regions in the Atlantic Ocean (19 out of 43) followed by the Pacific Ocean basin (n = 15), Arctic Ocean (n = 4), Southern Ocean (n = 3) and the Mediterranean Sea (n = 2) (Figure 3.1). Modeled ecosystems were primarily located in the Economic Exclusive Zones of countries (40 out of 43) with the exception of the Eastern Subtropical Pacific Ocean (Olson & Watters 2003), Antarctic peninsula (Erfan & Pitcher 2005) and Central Atlantic Ocean (Vasconcellos & Watson 2004) models. For comparison purposes,

models were allocated to only one latitude group following Pikitch et al. (2014), based on the geographic location of the Ecopath model (i.e. Tropical/Subtropical, Temperate or High latitude) or if it was an upwelling ecosystem (Table 3.1). The upwelling group consisted of only eastern boundary current upwelling ecosystems, which are unique in terms of forage fish contributions and dynamics (Pikitch et al. 2012).

Models were published in peer-reviewed journals (n = 13) or grey literature (i.e. academic, governmental, industrial reports, and working papers) (n = 30). The majority (20 out of 30) of models from grey literature were from the Fisheries Centre Research Report series published by the University of British Columbia (Vancouver, Canada), which undergoes an internal review process (Daniel Pauly, per. com, Fisheries Centre, University of British Columbia). Pedigree scores, which provide a measure of Ecopath model quality (Pauly et al. 2000, Christensen et al. 2008), were available for 15 of the 43 models and ranged from 0.240 to 0.675 with a mean and median score of 0.498 and 0.499 respectively. These scores are similar to those found in other studies (Morissette 2007, Pikitch et al. 2014) and are considered acceptable (Christensen & Walters 2004). Diet data for the majority of predator groups (78%, or 301 out of 384) were of good quality (i.e. either derived from diet studies in the model area or from a surrounding or similar region) based on the scoring methods in Essington & Plagányi (2013) (Figure 3.2). In addition, Figure 3.3 shows the attribute scores for predator and forage fish model group detail based on the methods of Essington & Plagányi (2013).

The majority (79%) of Ecopath models in this analysis had data on total catch (landings plus discards). The remaining 21% (9 out of 43) of the models only included landings data with no estimates of discards. Discards were assumed to be zero for these 9 models in the analysis. Thirty three percent (14 out of 43) of models included landings and discards data, and discards accounted for approximately 12% of the total catch of these models on average.

3.2.2 Predator production and diet dependencies

Diet data was compiled for seabird (n = 62), marine mammal (n = 132) and large predatory bony fish (n = 190) model groups in Ecopath models and the fraction of these predators' diet consisting of forage fish was analyzed. Because the detail of predator model

groups varied substantially between these ecosystem models (i.e. ranging from model groups of species with age-structure to highly aggregated groups of species) (Essington & Plagányi 2013), predators in ecosystem models with high predator detail (i.e. many model groups of a given predator category) were aggregated into single predator categories (i.e. seabirds, marine mammals, and large predatory bony fish) model groups. A weighted average of forage fish diet, based on the biomass of each predator group belonging to a particular predator category group in the ecosystem, was used to find the aggregated group forage fish dependence. This produced 43 aggregated forage fish diet values for each of the three major predator groups (i.e. one value for each specific predator category in each Ecopath model in this analysis).

The fraction of each predator group's production rate (t km^{-2} y^{-1}) supported by forage fish in every Ecopath model was calculated using equation 3.1 (Pikitch et al. 2014), which was originally derived from Hunsicker et al. (2010). The contribution by all forage fish prey to a particular predator's production (S_j) was found by the summation of the products from multiplying the proportion of forage fish group i in predator group j's diet ($D_{i,j}$) by the total ecosystem production of predator group j (P_j). Contributions to the production of the major predator categories (S_{pc}) in each model were found by summing up values from each predator (S_j) belonging to that predator category in each model using equation 3.2. Values from each Ecopath model were then analyzed across latitude types.

$$S_j = \sum_i D_{i,j} P_j \qquad\qquad\qquad (3.1)$$

$$S_{pc} = \sum_j \sum_i D_{i,j} P_j \qquad\qquad\qquad (3.2)$$

Although estimates of actual contributions to production rates (t km^{-2} y^{-1}) are meaningful to assess the magnitude in which forage fish contribute to predators, they do not take into account differences in the baseline production of these major predator categories or their current status across these human modified ecosystems. To account for this, the relative contributions forage fish make to production rates of predators in these predator categories were also assessed. This was done by calculating a weighted average of the diet dependency ($D_{i,j}$) values for each predator, based on biomass, belonging to each predator category in each model.

3.2.3 Dietary preferences and specialization of marine predators for forage fish prey

An index of electivity, the standardized forage ratio derived from Chesson (1983), was calculated to determine which prey items were most preferred by seabirds, marine mammals, and large predatory bony fishes in these ecosystem models. To allow for comparisons between models, prey model groups were combined into the following categories, forage fish (FF), non-forage fish (NFF), cephalopods (C), non-cephalopod benthic invertebrates (INV), zooplankton (Z), seabirds (SB), marine mammals (M) and other (O; i.e. discards, detritus, macroalgae). This allowed for prey items in each ecosystem model to be similarly aggregated. Although various electivity indices exist, the standardized forage ratio ($S_{i,j}$) was used as it is independent of prey density in an ecosystem and is commonly used in Ecopath software (Chesson 1983, Christensen et al. 2008). Values for this index range from 0 (relative avoidance) to 1 (exclusive feeding) and can be found using equation 3.3, where $r_{i,j}$ is defined as the proportion of prey i in predator j's diet and B_i is the proportion of prey i's biomass in the entire ecosystem. The denominator represents the sum of these ratios for all prey items for predator j, where n represents the number of prey groups in the model. Values of $S_{i,j}$ greater than $1/Bn$ indicate selection for the prey type, while values less than or equal to this indicate selection against the prey or random feeding respectively. For this analysis only the most preferred prey item (i.e. largest $S_{i,j}$ value) for each predator group was examined.

$$S_{i,j} = \frac{(r_{i,j}/B_i)}{\sum_{i=1}^{n} r_n / B_n} \qquad (3.3)$$

An omnivory index (OI_j) for each predator group, which specifically calculates the variance in trophic level of prey items (Christensen & Pauly 1992, Christensen et al. 2008), was also quantified. This index assesses if predator model groups exhibit specialized or generalist feeding habits. The OI_j was calculated for a predator group j according to Christensen et al. (2008) and listed in equation 3.4, by summing across all prey groups i (n) in the model, where TL_j represents the trophic level of predator group j, TL_i represents the trophic level of prey group i, and $D_{i,j}$ is as above. Trophic levels of predator and prey groups are based on the incremental trophic level concept according to Odum & Heald (1975), which is used to calculate TL in Ecopath models (Christensen et al. 2008).

$$OI_j = \sum_{i=1}^{n}(TL_i - (TL_j - 1))^2 \cdot D_{i,j} \qquad (3.4)$$

Once these indices were calculated for forage fish predator groups in all Ecopath models, comparisons were made between predator categories and across latitude groups.

3.2.4 Trophic similarities and overlap between forage fish predators and commercial fisheries

The mean trophic level of fisheries catch (mTL_Y) is commonly used as an index to evaluate the state of fisheries in ecosystems (Pauly et al. 1998a, Pauly & Watson 2005, Essington et al. 2006, Branch et al. 2010). Here it is used simply to estimate the mean trophic level in fisheries catches. Discards were included in this calculation. In a similar manner, the mean trophic level of predator consumption (mTL_q) index, derived by Morissette et al. (2012), was used to estimate the trophic level of prey items that marine predators are consuming in a given ecosystem. These indices were used in order to screen for potential latitude groups where fisheries and the major predator categories may be targeting prey at similar trophic levels. Using equation 3.5 (Pauly & Watson 2005, Morissette et al. 2012), the mTL_Y was found as the sum of multiplying the incremental trophic level of each fished model group c (TL_c) by the proportion of the catch (t km^{-2} y^{-1}) of model group c (Y_c) to the total catch of all species combined in that ecosystem (ΣY) for all items c. The mTL_Y was calculated in several ways for a given ecosystem to assess the differences in this value when 1) all fished model groups were included, 2) only fished finfish and cephalopods model groups were included and finally 3) only fished forage fish model groups were included.

$$mTL_Y \;=\; \Sigma_c \left(TL_c \cdot \left(\tfrac{Y_c}{\Sigma Y} \right) \right) \tag{3.5}$$

The mean trophic level of predator consumption (mTL_q) for each major forage fish predator group was calculated in each model using equation 3.6 (Morissette et al. 2012).

$$mTL_q \;=\; \Sigma_i \left(TL_i \cdot \left(\tfrac{\sum_{j=1}^{n} q_{i,j}}{\sum_{j=1}^{n} q_j} \right) \right) \tag{3.6}$$

The mTL_q of each forage fish predator group (i.e. seabird, marine mammal and large predatory bony fish) was computed in a manner similar to mTL_Y (Equation 3.5), except that the incremental trophic levels (TL_i) were multiplied in this case by the proportion of consumption of prey item i

by predator j ($q_{i,j}$) to the total consumption of predator j (q_j). Finally, a weighted average of mTL_q for predators in a given ecosystem model belonging to the same predator category (i.e. seabirds, marine mammals and large predatory bony fish) was calculated. This is a modification of the methods of Morissette et al. (2012), who gave equal weights to all predators of a certain category when calculating mTL_q, which does not allow for the mTL_q values of individual predator groups with higher biomass in an ecosystem to be more pronounced compared to those with scant biomass. Mean trophic level of fisheries catch and weighted mTL_q values for each of the predator categories were then analyzed by latitude groups.

Another approach used to assess the potential for conflicts between fisheries and forage fish predators was the trophic overlap index, derived by Kaschner & Pauly (2004). This index is based on both the dietary similarities between fisheries and predators and also the consumptive demands of these groups. Using equation 3.7, trophic overlap indices in models were calculated at two levels of predator aggregation, 1) between each predator category and fisheries, and 2) between all predator categories combined and fisheries. The overlap between fishery f and predator group j is expressed as $\alpha_{f,j}$ and is found by multiplying two terms.

$$\alpha_{f,j} = \left(\frac{2 \cdot \Sigma_i (D_{i,j} \cdot D_{i,f})}{\Sigma_i D_{i,j}^2 + \Sigma_i D_{i,f}^2} \right) \cdot \left(\frac{q_j}{(q_j + C_f)} \cdot \frac{Y_f}{(q_j + Y_f)} \right) \qquad (3.7)$$

The first term expresses the similarity in diet and catch between predator group j and fishery f in sharing prey species i, where $D_{i,j}$ is similar as above and $D_{i,f}$ represents the proportion of prey i to fishery f. This term was then multiplied by the product of two proportions, the proportion of total prey consumption by marine predator j (q_j) and the proportion of total fishery f catches (Y_f) both respectively over the total consumption of prey i (predator consumption (q_j) + fisheries catch (Y_f)) in the ecosystem. When calculating this index for aggregated groups (i.e. predator categories or all predators), a weighted average of $D_{i,j}$ based on biomass of predator groups and added the consumption terms (q_j) for all applicable predator groups was used. This index ranges from 0 (no overlap) to 0.250 (complete overlap) and values were compared by latitude group.

3.2.5 Data management and statistical analysis

All data and output from Ecopath models used in this analysis (i.e. diet data, consumption rates, production rates, and biomass) were either previously transcribed into Microsoft$^{©}$ Excel spreadsheets from an existing database (Pikitch et al. 2014), or were manually entered into new spreadsheets following the methods in Pikitch et al. (2014). All indices were calculated in Excel spreadsheets. Notched box plots of diet data and indices were created using R statistical software (CRAN R, version 2.15.0, package lattice, www.R-project.org/), and statistical significance was inferred visually (McGill et al. 1978, Chambers et al. 1983).

To determine relationships between the percentage of forage fish in the diet of each predator category as a result of the proportion of forage fish biomass out of the total fish and cephalopod biomass in the ecosystem, linear regression models (lm function) were calculated using the R commander (Rcmdr), a graphical user interface for the R statistical software (Fox 2005).

3.3 Results
3.3.1 Predator production and diet dependencies

Baseline production rates of forage fish predator groups varied by category and latitude group (Table 3.2). Median production rates of large predatory bony fish ranged from 0.403 to 2.051 t km^{-2} y^{-1} and were often 1-2 orders of magnitude larger than those for seabirds (range = 0.0011 - 0.0077 t km^{-2} y^{-1}) and marine mammals (range = 0.002 - 0.013 t km^{-2} y^{-1}) in all latitude groups (Table 3.2). A similar result was found when evaluating the production rates supported by forage fish, with the largest contributions derived for large predatory bony fish (Table 3.3). Regardless of predator category, the largest median production rates supported by forage fish were found in high latitudes and the greatest single contributions in each predator category were found in upwelling ecosystems (Table 3.3).

To account for the large differences in baseline predator production rates observed in these ecosystems, predator diet dependence (i.e. the proportion of predator production rates supported by forage fish) was also assessed. Combining diet dependencies for each predator group across all ecosystem models (n = 43), notched box plots suggested that seabirds had a significantly greater proportion of forage fish in their diets (median = 0.48, 95% CI = 0.40 - 0.55) compared to marine mammals (median = 0.27, 95% CI = 0.21 - 0.34) and large predatory

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bony fish (median = 0.24, 95% CI = 0.20 - 0.35) (Figure 3.4). Seabirds in upwelling ecosystems had the highest forage fish diet dependency values (median = 0.89, 95% CI, 0.27 - 0.95) for any predator category and in any latitude group, except for large predatory bony fish in upwelling ecosystems (Figure 3.5). The lowest forage fish diet dependence values for seabirds were found in tropical/subtropical latitudes (0.37, 95% CI = 0.26 - 0.54) and median values increased poleward, although this was not statistically significant (Figure 3.5). For marine mammals, no significant differences in diet dependency values were found, with median values greatest in high latitudes (0.37, 95% CI = 0.22 - 0.47) followed by upwelling (0.32, 95% CI = 0.07 - 0.70), tropical/subtropical (0.25, 95% CI = 0.13 - 0.43) and temperate (0.20, 95% CI = 0.10 - 0.33) latitudes (Figure 3.5). Median diet dependency values for large predatory bony fish were greatest in upwelling ecosystems (0.47, 95% CI = 0.06-0.83) and the smallest in tropical/subtropical latitudes (0.20, 95% CI = 0.12-0.38), with no significant differences in diet dependency found between latitude groups (Figure 3.5).

In addition to diet dependency results, statistically significant positive relationships among all three predator categories were found between the proportion of forage fish in predators' diets and the proportion of forage fish biomass in the ecosystem (i.e. forage fish biomass over the total fish and cephalopod biomass in an ecosystem) (Linear model: $r^2 = 0.24 - 0.28$, $p < 0.001$ for each predator category (Figure 3.6). When examining this relationship across latitude groups, statistically significant positive regressions were only found for seabirds ($r^2 = 0.49$, $p = 0.016$) and marine mammals ($r^2 = 0.73$, $p = 0.002$) in high latitudes and large predatory bony fish ($r^2 = 0.44$, $p = 0.01$) in temperate latitudes (Table 3.4).

3.3.2 Dietary preferences and specialization of marine predators for forage fish prey

Forage fish were the most preferred prey item for 32% of seabirds (21 out of 65), 18% of marine mammals (24 out of 130) and 26% of large predatory bony fish (50 out of 189) in all ecosystem models combined, based on the Chesson electivity index (Chesson 1983). Across latitude groups, only 24 to 39% of seabirds, 6 to 23% of marine mammals, and 21 to 36% of large predatory bony fish had forage fish as their most preferred prey item (Figure 3.7). Forage fish were the preferred prey type for 39% of seabirds (7 out of 18) in tropical/subtropical latitudes, and this percentage decreased by latitude in a poleward direction (Figure 3.7). For

marine mammals the opposite trend was found, with 23% of marine mammals (14 out of 62) selecting forage fish prey in high latitudes and the percentage decreasing towards the equator (Figure 3.7). No trend was found for large predatory bony fish, with 36% (24 out of 67) selecting forage fish in temperate latitudes and 21% selecting forage fish in both high latitude (9 out of 43) and tropical/subtropical latitudes (12 out of 57). In upwelling ecosystems, 33% of seabirds (3 out of 9), 6% of marine mammals (1 out of 17), and 24% of large predatory bony fish (5 out of 21) selected forage fish as their most preferred prey. In upwelling and high latitude models, cephalopods were the most preferred prey item for the majority of predators in all predator categories (Figure 3.7).

Across all ecosystem models combined, omnivory index values for all predators were relatively low and not significantly different from one another based on the notched box plots (Figure 3.8). Marine mammals were the most specialized predator category (median OI = 0.17, 95% CI = 0.17-0.21, n = 130) overall, followed by large predatory bony fish (median OI = 0.19, 95% CI = 0.19-0.23, n = 189) and seabirds (median OI = 0.21, 95% CI = 0.18-0.28, n = 65). When grouped by latitude type, OI values for all predator categories were similarly low (Figure 3.9). Seabirds in upwelling ecosystems generally had the lowest OI values (median OI = 0.05, 95% CI = 0.03-0.25 n = 8), but this was not significantly different from other predators in that latitude group based on notched box plots (Figure 3.9).

3.3.3 Trophic similarities and overlap between forage fish predators and commercial fisheries

Globally, no significant differences between the mean trophic level of forage fisheries catches and predator consumption were found when combining indices from all ecosystem models (Figure 3.10). Mean trophic level of marine mammal consumption (median = 3.20, 95% CI = 3.07-3.29) was significantly higher than values for seabirds (median = 2.87, 95% CI = 2.80-3.00) and large predatory bony fish (median = 2.90, 95% CI = 2.74-2.98) based on the notched box plots. Mean trophic level of catch for all fisheries (median = 3.24, 95% CI = 3.13-3.49), all finfish fisheries (median = 3.3, 95% CI = 3.21-3.54) and all forage fisheries (median = 3.05, 95% CI = 2.83-3.10) were not significantly different from each other (Figure 3.10).

Across latitude groups, no differences were found between the mTL_q for any predator and the mTL_Y of all forage fisheries based on the notched box plots (Figure 3.11). Significant differences between mTL_Y and mTL_q values were found in tropical/subtropical (i.e. between finfish fisheries and seabirds), temperate (i.e. between finfish fisheries and both seabirds and large predatory bony fish) and high latitude (i.e. between all fisheries and large predatory bony fish) groups. The only significant differences between the mTL_q of predators were found in temperate latitudes, where mTL_q of marine mammals (median = 3.31, 95% CI = 3.16-3.52) was significantly greater than seabirds (median = 2.94, 95% CI = 2.69-3.08) and large predatory bony fish (median = 2.97, 95% CI = 2.80-3.09) (Figure 3.11). No differences between fisheries and or predators were found in upwelling ecosystems and high latitudes.

No evidence of strong overlap between specific predator categories and fisheries were found in ecosystem models, as 95% (123 out of 129) of overlap index values were less than half (i.e. < 0.125) of the value for complete overlap (i.e. 0.250) (Figure 3.12). In addition, predator groups were not significantly different from each other in any latitude group. Significantly higher overlap values were found between marine mammals in upwelling compared to temperate ecosystems, and large predatory bony fish in tropical/subtropical ecosystems compared to high latitudes based on the notched box plots (Figure 3.12). Median trophic overlap values between large predatory bony fish and fisheries were greatest in upwelling and tropical/subtropical latitudes and decreased with increasing latitude (Figure 3.12). Across latitude types, seabirds had a consistently low overlap with fisheries, although the largest overlap value (0.199) was found in the Senegambia tropical/subtropical latitude model between a seabird group and fisheries.

Finally, when examining trophic overlaps between all predator categories combined and fisheries across latitude groups, values in upwelling ecosystems covered the largest range (median = 0.054, 95% CI = 0.001-0.213), from almost no overlap to almost complete overlap (Figure 3.13). Although overlap values for tropical/subtropical (median = 0.044, 95% CI = 0.03-0.06) latitude group were significantly greater than temperate (median = 0.006, 95% CI = 0.004-0.102) and high latitude (median = 0.003, 95% CI = 0.001-0.009) groups based on the notched box plots, these overlap values were all quite low.

3.4 Discussion
3.4.1 Characterizing forage fish predators across latitudes

Forage fish species make up a large fraction of the diets of many marine predators (Pikitch et al. 2014). In this study, seabirds generally had the highest proportion of forage fish in their diets compared to marine mammals and large predatory fish across every latitude group, although significant difference based on notched box plots were not always found (Figure 3.5). This was particularly apparent in upwelling ecosystems where seabird diets consisted almost entirely of forage fish and represented a significantly greater fraction of the diet than for marine mammals but not large predatory bony fish. The importance of forage fish prey to seabirds is well documented based on empirical studies from a variety of ecosystems throughout the world (e.g. Cury et al. (2011), Österblom et al. (2008)), and especially in upwelling ecosystems (Anderson et al. 1982, Muck & Pauly 1987, Crawford et al. 2006, Becker et al. 2007, Elliott et al. 2007, Crawford et al. 2008). A high degree of trophic specialization among seabirds were found in upwelling ecosystems, with 33% selecting forage fish as their most preferred prey item. These factors (i.e. high specialization and preference for forage fish) may partially account for the strong empirical relationships shown between forage fish availability and factors affecting seabird populations. Forage fish content in the diets of marine mammals and large predatory bony fish did not differ significantly between latitude groups. In addition, these predator categories showed similar degrees of specialization.

Forage fish were selected as the most preferred prey item for ≥24% of seabirds, ≥6% of marine mammals and ≥21% of large predatory bony fishes in each latitude group (Figure 3.7). This is not surprising given the dietary importance of these prey items to these predator groups globally (Pauly et al. 1998b, Walter & Austin 2003, Cury et al. 2011, Logan et al. 2011, Magnussen 2011). In addition, there is a growing body of empirical studies demonstrating selection of forage fish species by seabirds (Golet et al. 2000, Burke & Montevecchi 2008), marine mammals (Lawson et al. 1998, Lindstrøm et al. 1998, Meynier et al. 2008, Spitz et al. 2012), and large predatory bony fish (Pinnegar et al. 2003, Rudershausen et al. 2005, Mahe et al. 2007, Spitz et al. 2013). In the majority of these studies, the authors state that selection for forage fish was likely due to their availability in the ecosystem (i.e. spatially and temporally) and or their high nutritional quality relative to other prey items (Van Pelt et al. 1997, Österblom et al.

2008, Spitz et al. 2010). Changes in the availability of nutritious forage prey species have been implicated as important factors in the health of some predators (Trites & Donnelly 2003, Wanless et al. 2005, Burke & Montevecchi 2008, Grèmillet et al. 2008, Engelhard et al. 2013). More comprehensive empirical analyses are needed to corroborate these results, but it is interesting that estimates from this study of forage fish selection by harp seals (*Pagophilus groenlandicus*) in the Newfoundland (Heymans & Pitcher 2002) and Barents Sea (Blanchard et al. 2002) were consistent with those of empirical studies conducted for these predators in those regions (Lawson et al. 1998, Lindstrøm et al. 1998). Unfortunately, no other empirical studies have been conducted in the same regions as the ecosystem models used in this analysis, so these results cannot be fully validated.

3.4.2 Trophic similarities and overlap between forage fish predators and commercial fisheries

This study found that forage fisheries, seabirds, marine mammals, and large predatory bony fish were targeting similar trophic levels of prey in each latitude group. This does not mean that index values were always similar between these groups in every ecosystem model in this analysis, as there were a variety of ecosystems where the mean trophic levels of fisheries catch and predator consumption were different. Differences in mTL_Y and mTL_q of marine mammals has been demonstrated before by Morissette et al. (2012) for several Ecopath models. This study builds on the initial work of Morissette et al. (2012) in four ways, by 1) extending the application of mTL_q to include seabirds and large predatory bony fish, 2) including other estimates of mTL_Y, such as mTL_Y of finfish fisheries catch and forage fish fisheries catch, 3) using more Ecopath models, and 4) making comparisons based on latitudinal scales. Analyzing the mTL_q for all of the major forage fish predators and the mTL_Y for forage fisheries seemed especially warranted as 42% (18 out of 43) of our ecosystem models had a forage model group represented the single largest fishery (t km^{-2} y^{-1}) in the ecosystem, and more importantly, forage fisheries represent a large an growing fraction of the global commercial catch (Alder et al. 2008, FAO 2012). This approach may be useful in both screening for ecosystems where potential trophic conflicts between fisheries and marine predators may occur, and also identifying predators which may interact with fisheries for similar prey, especially in cases where new forage fisheries are

proposed and there is limited data on marine predators. In addition, little change (<0.5) in mTL_Y values was found when discards were removed from these calculations for the 14 Ecopath models that had both landings and discard data (Figure 3.14). In these 14 models, discards represented only 12% of the catch on average. Global discards represent approximately 8% of the marine fisheries catch by weight but this varies greatly among species and ecosystems (Kelleher 2005).

Relatively low overlap between fisheries and marine predator categories were found at latitudinal scales, which is consistent with the results from other global analyses for seabirds and marine mammals (Kaschner & Pauly 2004, Kaschner et al. 2006, Karpouzi et al. 2007). Interestingly, overlap index values for large predatory bony fish were not significantly different from those for seabirds and marine mammals. While analyzing overlap index values for specific predator groups may be informative, this approach ignores the fact that marine predators do not act in isolation from each other in fished ecosystems. To account for this, overlap index values between all predators (i.e. seabirds, marine mammals, and large predatory bony fish) combined and fisheries were also analyzed. These results showed similarly low overlap values between marine predators and fisheries across latitudes, however overlap values seemed to decrease with increasing latitude (Figure 3.12). At ecosystem scales, predator groups in several ecosystems had relatively high overlap (i.e. >0.125) with fisheries, including seabirds in Senegambia ($\alpha_{f,j}$ = 0.199), marine mammals in southern Benguela current ($\alpha_{f,j}$ = 0.137), and large predatory fish in the northern and central Adriatic Sea ($\alpha_{f,j}$ = 0.200), northern Humboldt current ($\alpha_{f,j}$ = 0.191), northwestern Mediterranean Sea ($\alpha_{f,j}$ = 0.166), and Gulf of California ($\alpha_{f,j}$ = 0.127). In addition, there was good agreement between the overlap values calculated in this study and those from Morissette et al. (2012) for marine mammals in the same or similar ecosystem models (i.e. Bering Sea, Northern Gulf of St. Lawrence, Eastern Subtropical Pacific, Southern Benguela current). Analyses at even finer scales than ecosystems may be warranted to truly understand potential overlap between marine predators and fisheries, especially if hotspots between predators and forage fish prey can be identified (Davoren 2013). For instance, empirical studies have demonstrated that high overlap and potential conflicts can occur at smaller spatial scales for dolphins (Gómez-Campos et al. 2011, Morteo et al. 2012), or near seabird colonies (Boersma et

al. 2002, Crawford et al. 2008, Frederiksen et al. 2008, Bertrand et al. 2012) and pinniped rookeries (Staniland et al. 2012, Riet-Sapriza et al. 2013).

3.4.3 Challenges and opportunities from synthesizing "recycled" ecosystem models to calculate ecological indices

There are several challenges when using ecosystem models to inform fisheries management policies based on their assumptions, scope, and the complexity of the ecosystems being modeled (FAO 2007, Fulton 2010). These challenges are particularly apparent when syntheses use "recycled" models (i.e. models that are repurposed for uses other than their original application) to develop management advice (Essington & Plagányi 2013). However, these types of syntheses may provide valuable opportunities and insights for managers (Smith et al. 2011, Pikitch et al. 2012), while, of course, acknowledging their shortcomings (Essington & Plagányi 2013). Regardless, it is important to recognize that ecosystem models are the model authors' best attempt to represent an ecosystem using the best available data. Detailed descriptions of the assumptions, utility, and shortcomings of Ecopath models are described elsewhere (e.g. Christensen & Walters (2004), Plagányi & Butterworth (2004)).

Ecopath models are one of the most commonly used ecosystem models in the world, requiring a wealth of data for their creation (Christensen & Walters 2004, Fulton 2010, Colléter et al. 2013). In this study, data and output from several parameters (i.e. diet data, biomass, consumption and catch) published in Ecopath models were used in order to calculate a variety of predator and fishery indices in different areas around the world. The actual models (i.e. ".ewe" files) were not used, but instead the data in model publications were utilized. This analysis was constrained to only include Ecopath models, so that differences in parameters (or their estimation) was not due to differences in model software type, but rather were desired by model authors based on their ecosystem's characteristics and available information (Pikitch et al. 2014). Importantly, this analysis relied on the use of diet data, which were found to be of relatively high quality (i.e. from studies conducted in the model area or surrounding regions (Essington & Plagányi 2013)). As Ecopath models only represent temporal snapshots of an ecosystem at a given spatial scale, our reasoning followed that of Pikitch et al (2014), in that synthesizing models by latitude groups would reduce the effects of stochastic uncertainty. This study

emphasized the idea that Ecopath models can serve as a valuable repository for ecological data for scientists (Colléter et al. 2013), even if the model software is not actually available for use. As such, syntheses such as this may provide timely information to ecosystem managers when comprehensive studies of predators are not available in their ecosystem and be used to inform their own ecosystem modeling efforts.

Understanding the role forage fish play in the healthy functioning of ecosystems, particularly in terms of predator-prey dynamics, is a major consideration in ecosystem-based forage fisheries management (Pikitch et al. 2004, Pikitch et al. 2012, Essington & Plagányi 2013). However, data on marine predators habits, predator-prey dynamics, and the shapes of functional responses are often sparse (Pitcher et al. 2009, Tallis et al. 2010, Cury et al. 2011), especially in tropical ecosystems (Bundy et al. 2012). In this study, it was demonstrated how data collected from Ecopath model publications can be used to effectively calculate several indices for forage fish predators and fisheries in these ecosystems. This approach may be useful in guiding future syntheses with Ecopath models in order to inform ecosystem-based fisheries management.
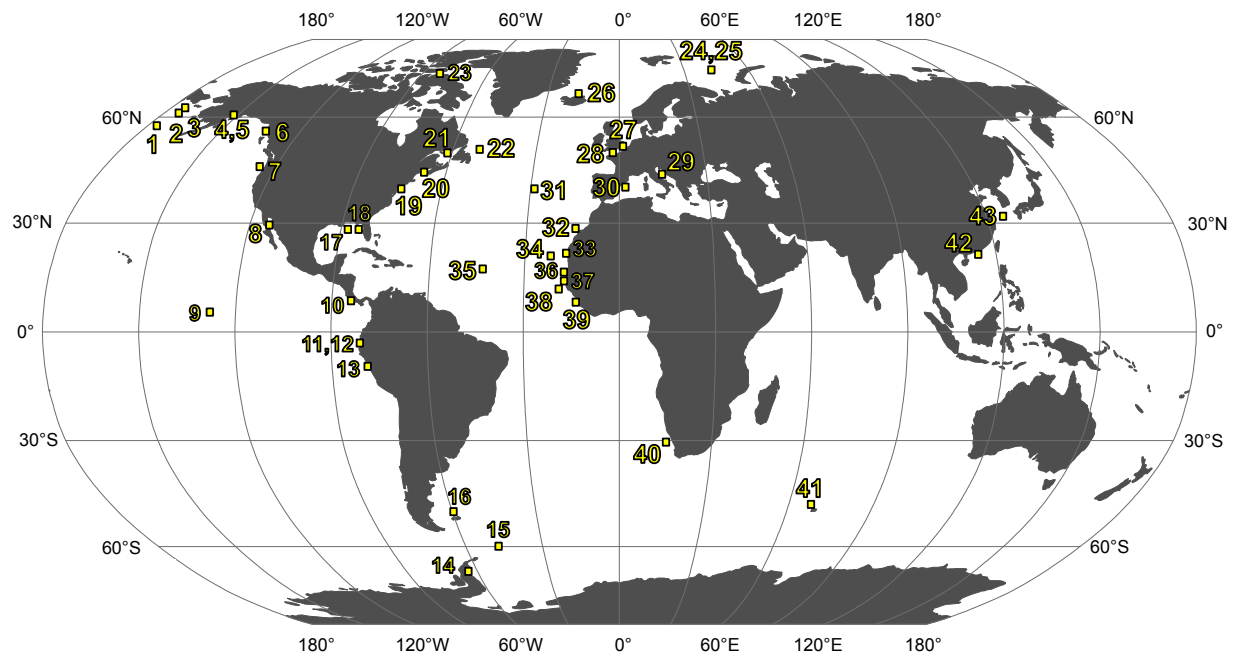
Figure 3.1 Map of 43 Ecopath models used in this study. Model numbers refer to those in Table 3.1. Yellow squares indicate the approximate location of each model.
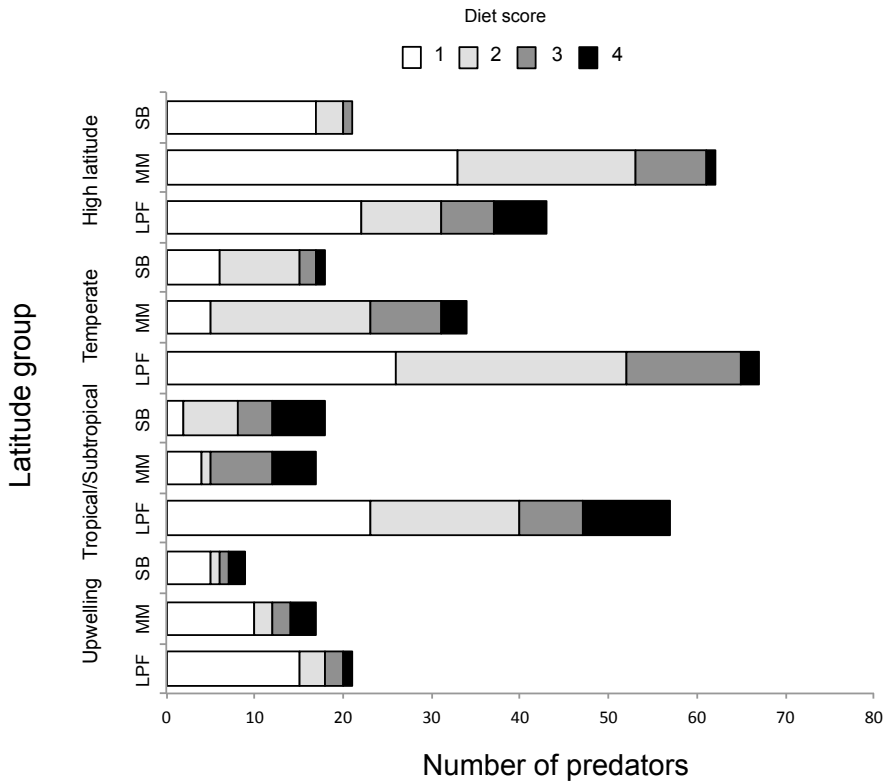
Figure 3.2 Quality of diet data for seabirds (SB), marine mammals (MM), and large predatory bony fish (LPF) across latitude groups based on Essington & Plagányi (2013), where 1 = diet data from studies in that region, 2 = diet data from studies nearby or similar regions, 3 = diet data largely from summaries or standardized diets, and 4 = diet data sources not revealed.
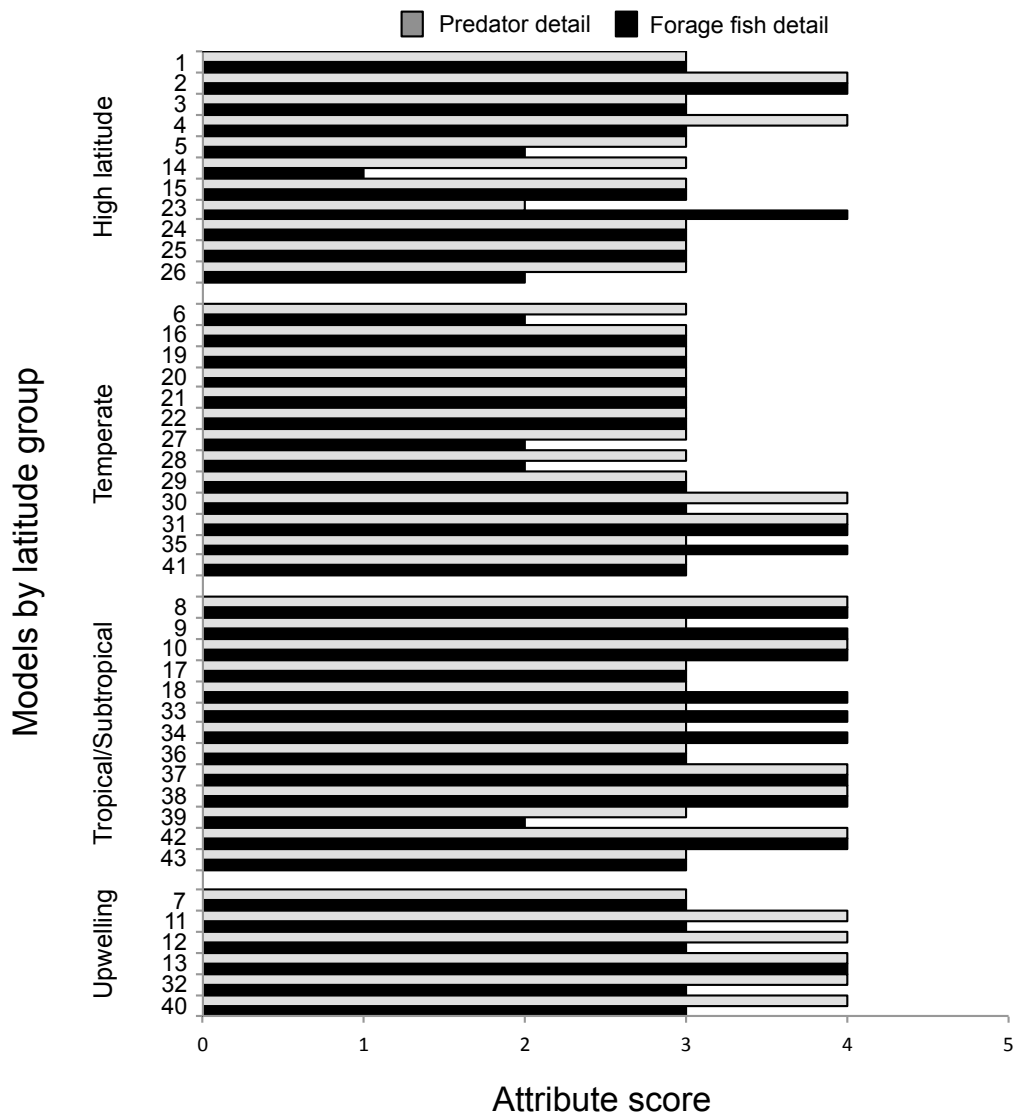
Figure 3.3 Attribute scores for ecosystem models used in this synthesis revealing the detail of predator and forage fish model groups based on Essington & Plagányi (2013). Model numbers correspond to those in Table 3.1. Scores include: 1 = model groups grouped by species with age structure, 2 = model groups grouped by species with no age structure, 3 = some model groups grouped by species and others aggregated and 4 = key forage fish or predator groups aggregated.
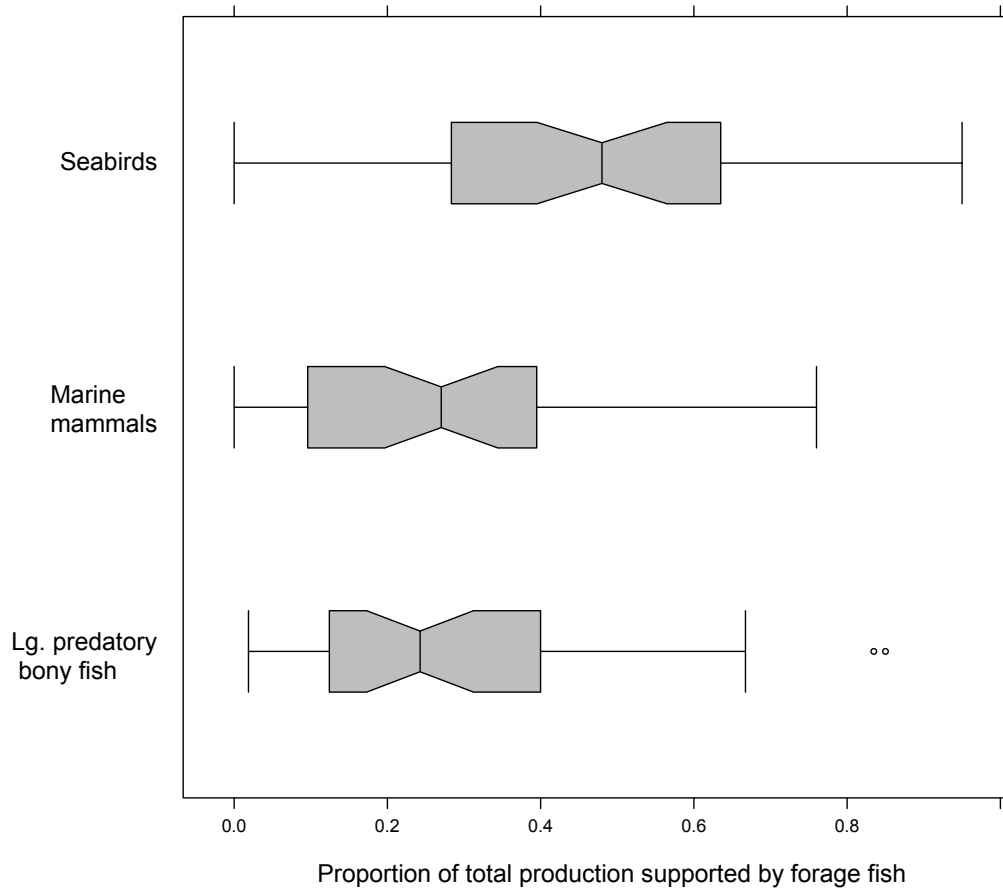
Figure 3.4 Notched box plots of the proportion of predator production supported by forage fish for each predator group in all ecosystem models combined. Lines inside box plots represent the median values, while the left and right segments represent the 0.25 and 0.75 quartiles respectively. Open circles represent data outliers identified by the R statistical software.
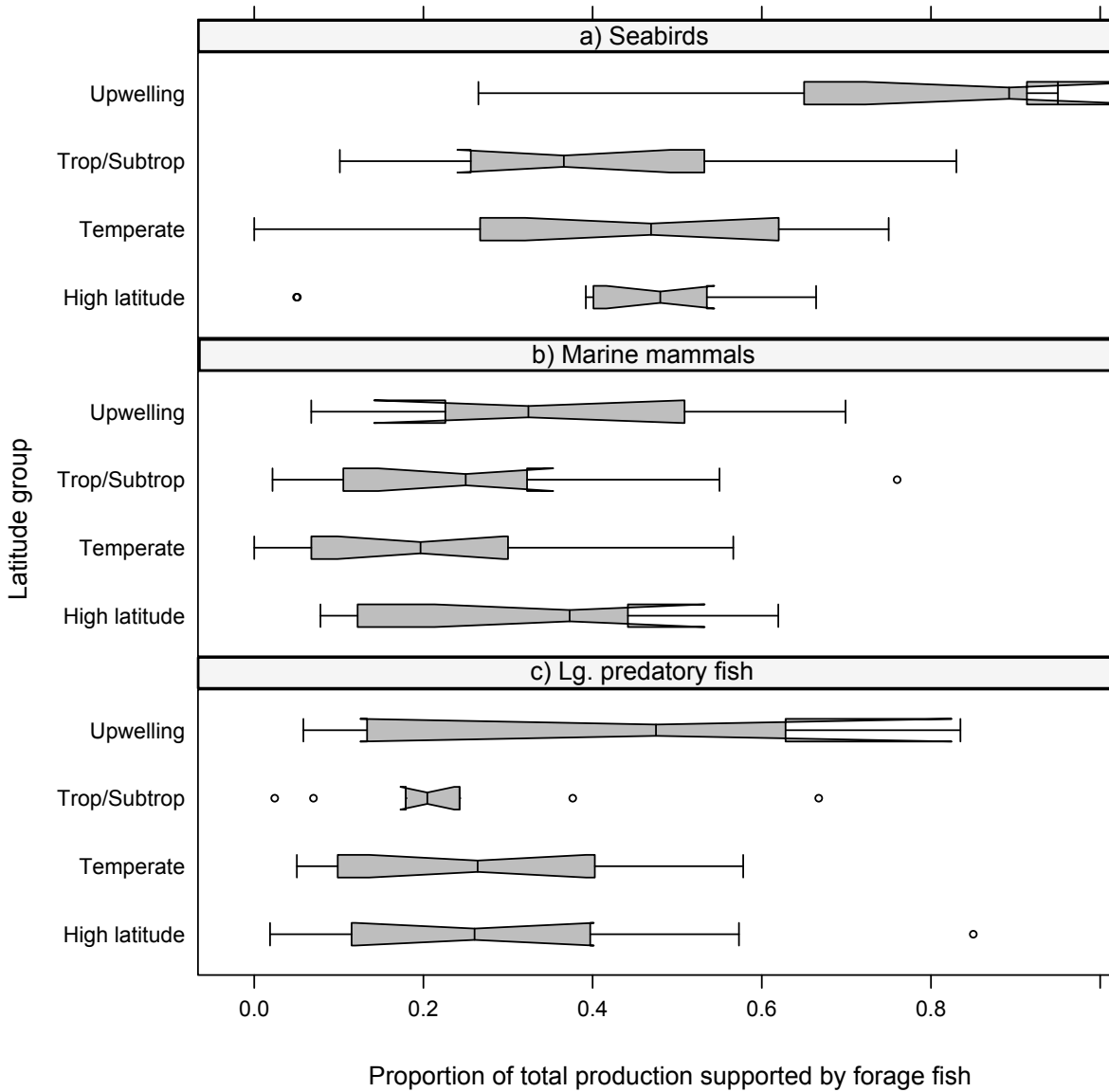
Figure 3.5 Notched box plots of the proportion of predator production supported by forage fish for a) seabirds, b) marine mammals, and c) large predatory bony fish across latitude groups. Lines inside box plots represent the median values, while the left and right segments represent the 0.25 and 0.75 quartiles respectively. Open circles represent data outliers identified by the R statistical software.
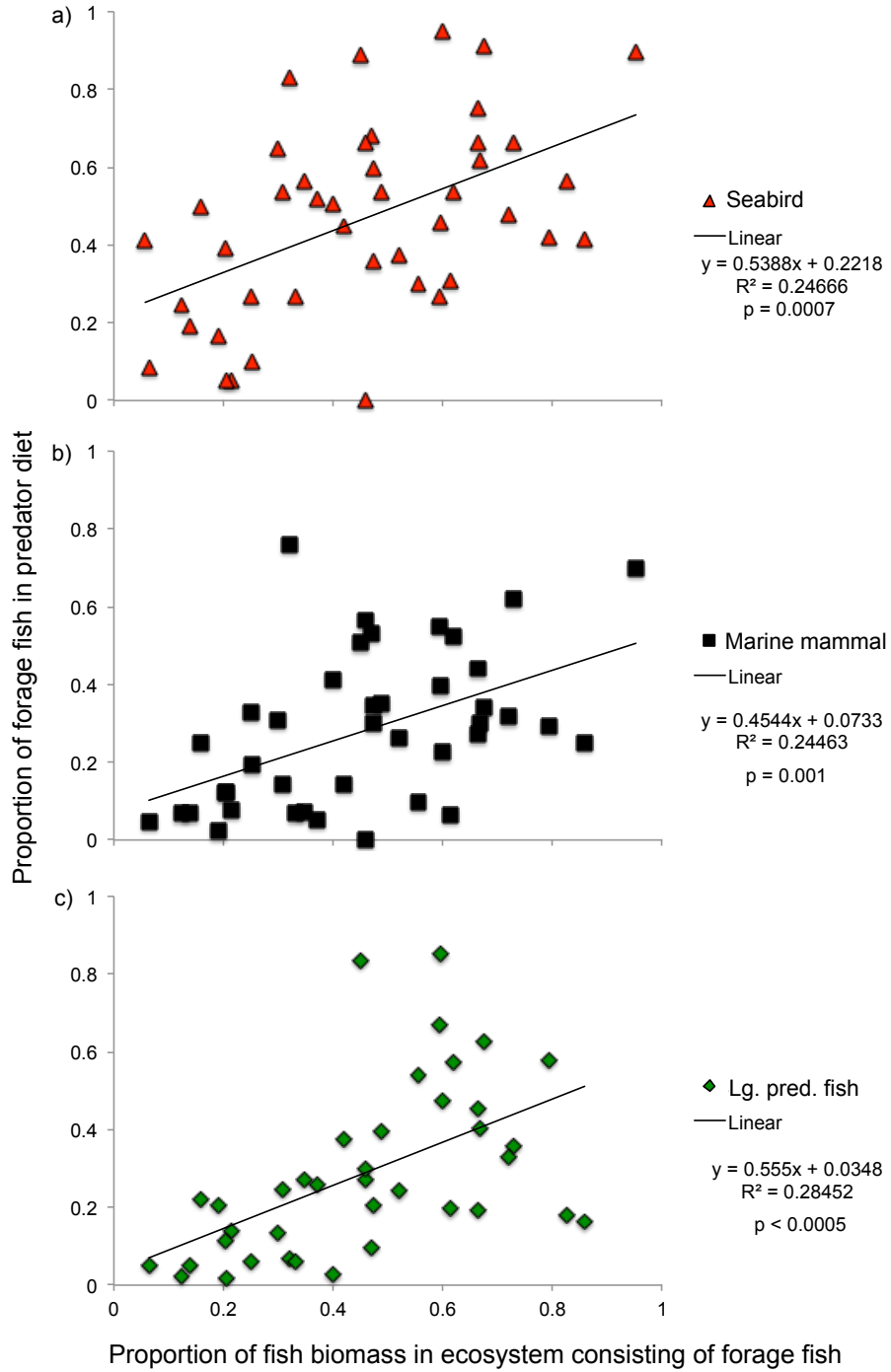
Figure 3.6 Linear regressions showing the positive relationships between the proportion of forage fish in the diet of a) seabirds, b) marine mammals, and c) large predatory bony fish as a result of the proportion of total fish biomass in the ecosystem consisting of forage fish.

a) Seabirds

b) Marine mammals

c) Lg. Predatory bony fish

Percentage of predators

High latitude   Temperate   Tropical/ Subtropical   Upwelling
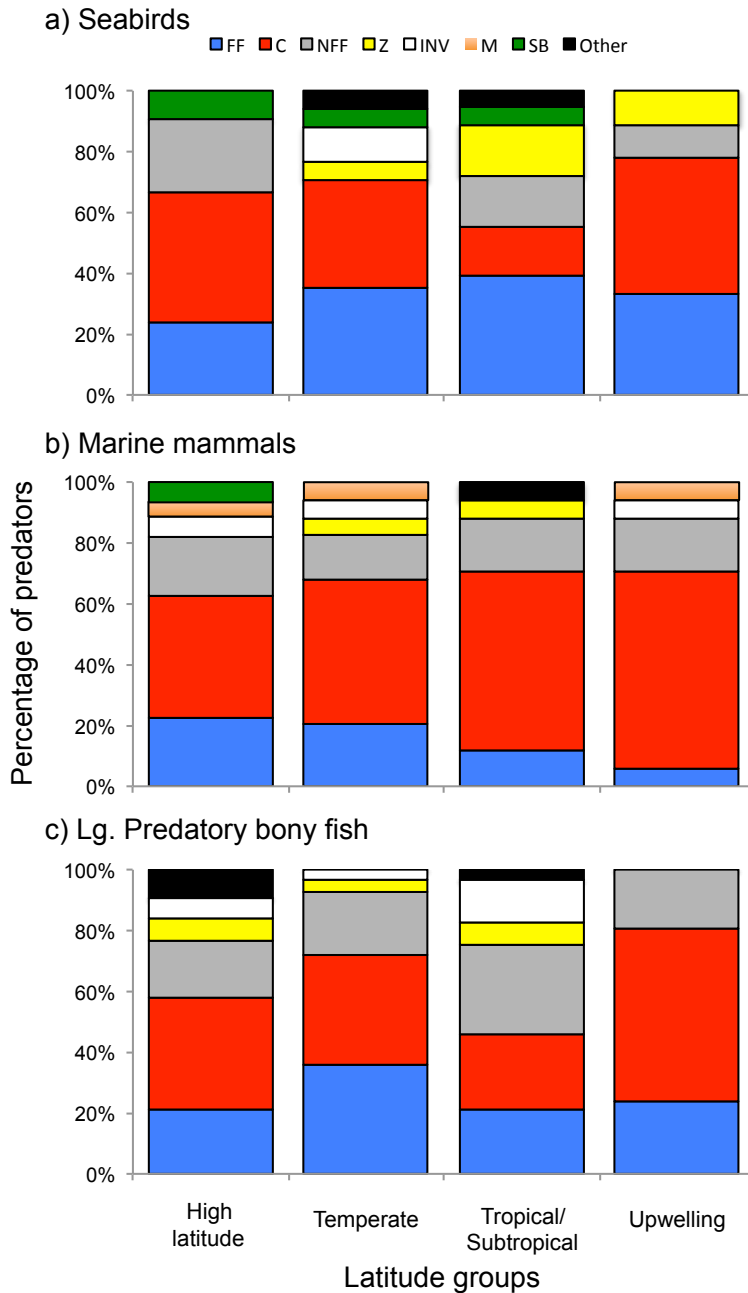
Latitude groups

Figure 3.7 Percentages of a) seabirds, b) marine mammals, and c) large predatory bony fish predators in each latitude group with their most selected prey type. Prey types include forage fish (FF), cephalopods (C), non-forage fish (NFF), zooplankton (Z), non-cephalopod benthic invertebrates (INV), marine mammals (M), seabirds (SB) and miscellaneous prey types including detritus, discards and macroalgae (Other).

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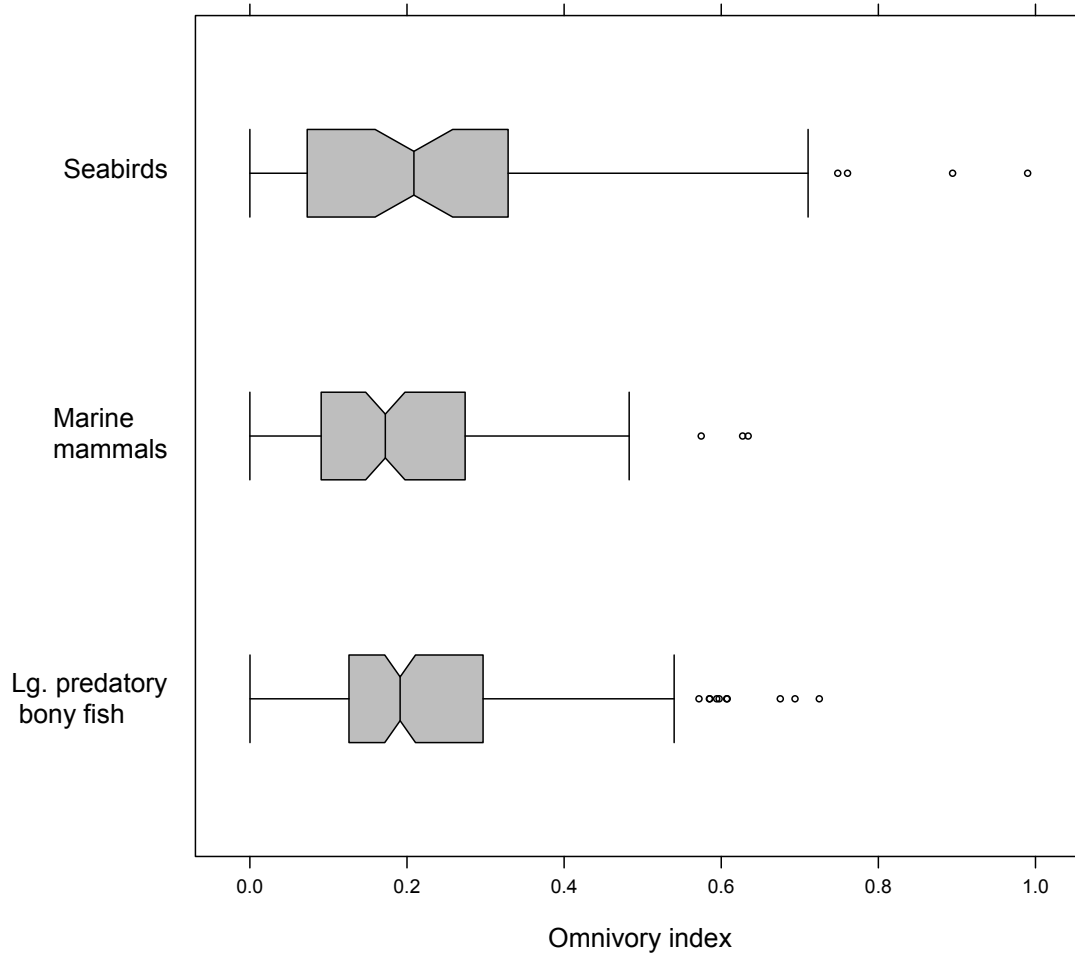
Figure 3.8 Notched box plots of omnivory index values for all seabirds, marine mammals, and large predatory bony fish across all ecosystem models. Lines inside box plots represent the median values, while the left and right segments represent the 0.25 and 0.75 quartiles respectively. Open circles represent data outliers identified by the R statistical software.
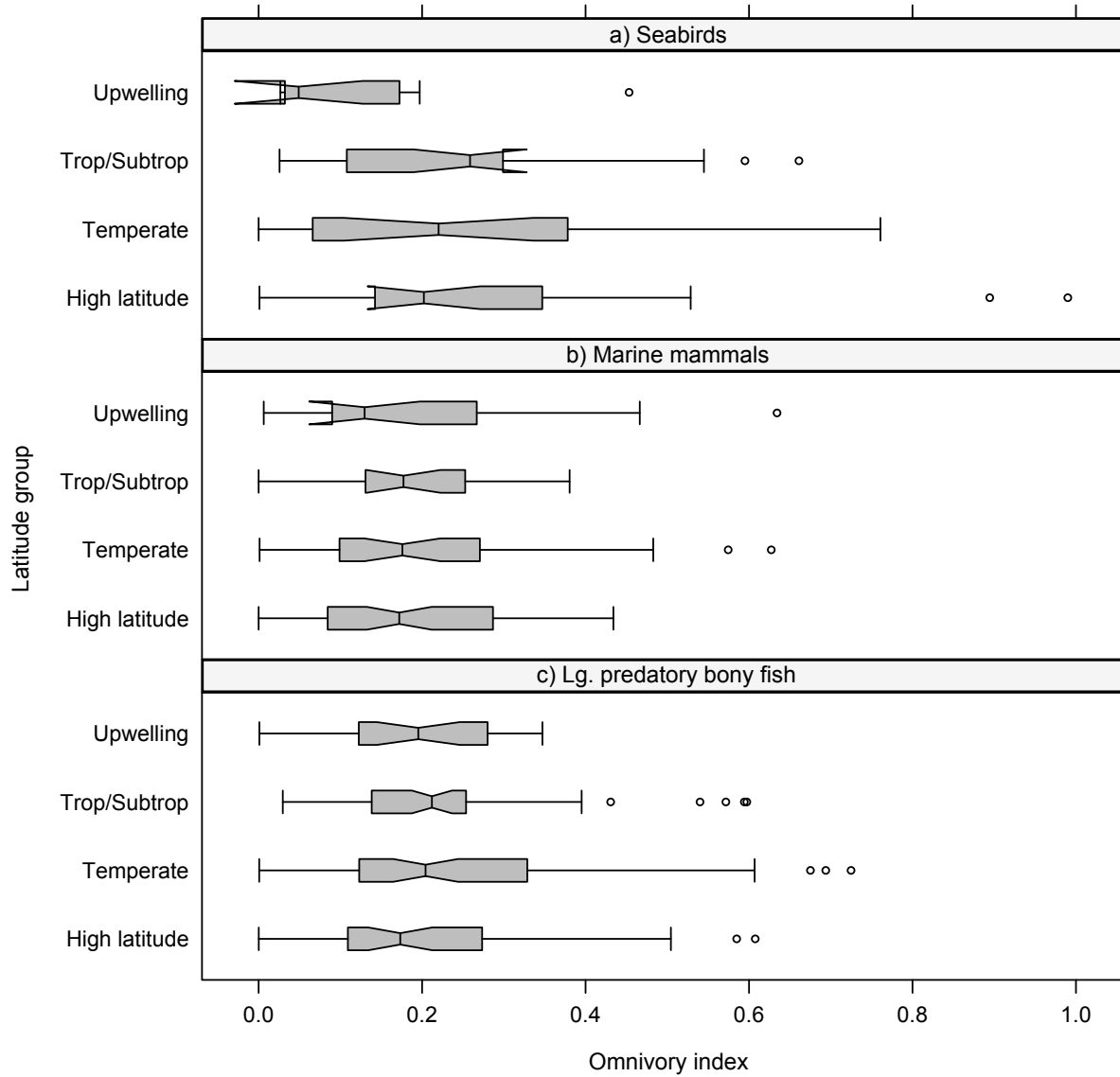
Figure 3.9 Notched box plots of omnivory index values for a) seabirds, b) marine mammals, and c) large predatory bony fish across latitude groups. Lines inside box plots represent the median values, while the left and right segments represent the 0.25 and 0.75 quartiles respectively. Open circles represent data outliers identified by the R statistical software.
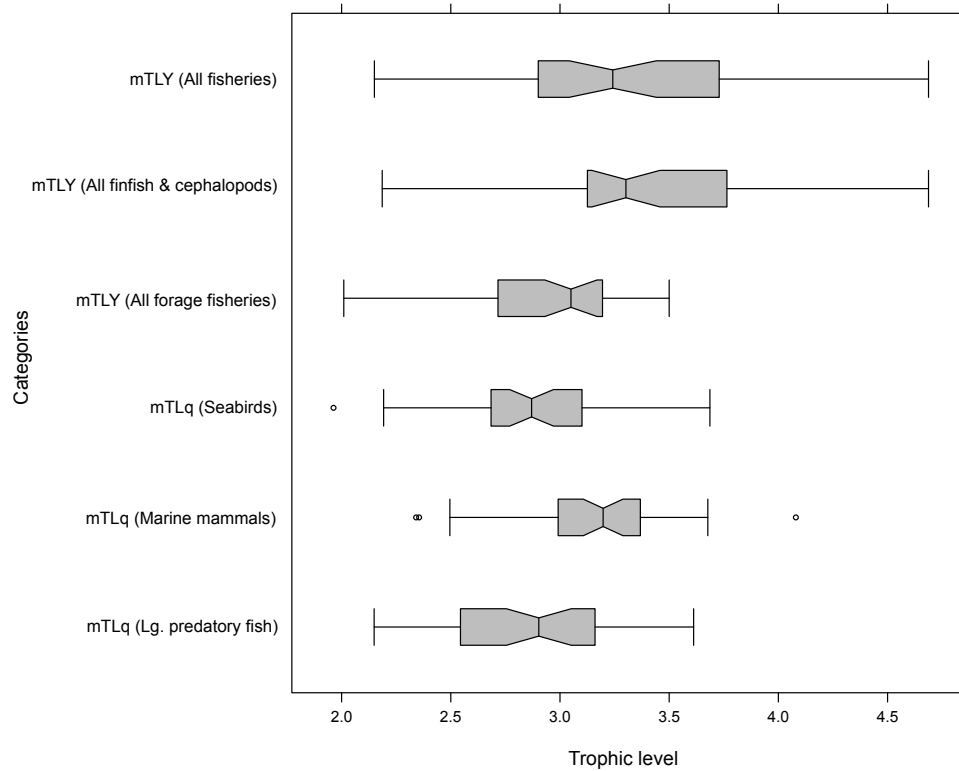
Figure 3.10 Notched box plots of mean trophic level of catch (*mTL$_Y$*) and predator consumption (*mTL$_q$*) for all 43 Ecopath models combined. Lines inside box plots represent the median values, while the left and right segments represent the 0.25 and 0.75 quartiles respectively. Open circles represent data outliers identified by the R statistical software.
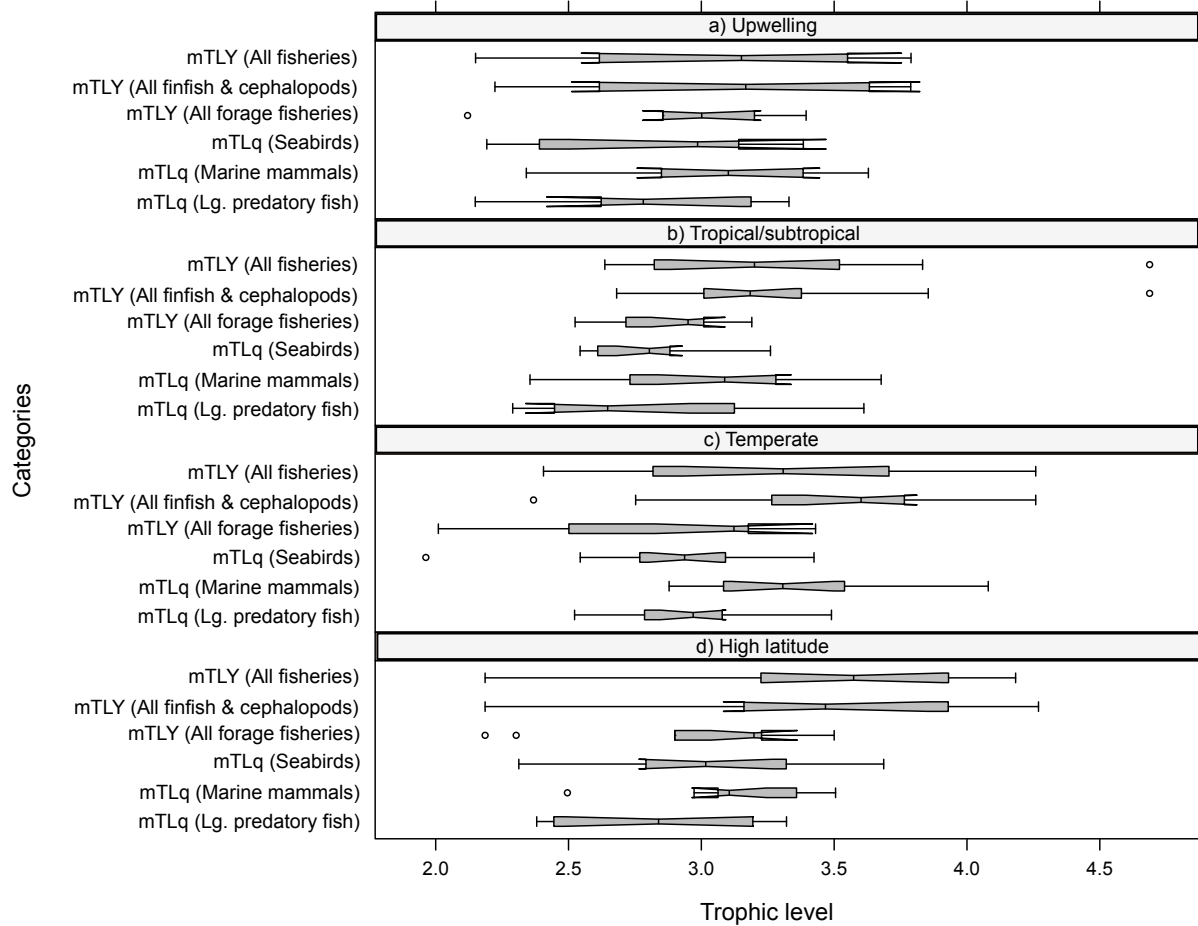
Figure 3.11 Notched box plots of mean trophic level of catch (mTL_Y) and predator consumption (mTL_q) for a) upwelling, b) tropical/subtropical, c) temperate, and d) high latitude groups. Lines inside box plots represent the median values, while the left and right segments represent the 0.25 and 0.75 quartiles respectively. Open circles represent data outliers identified by the R statistical software.
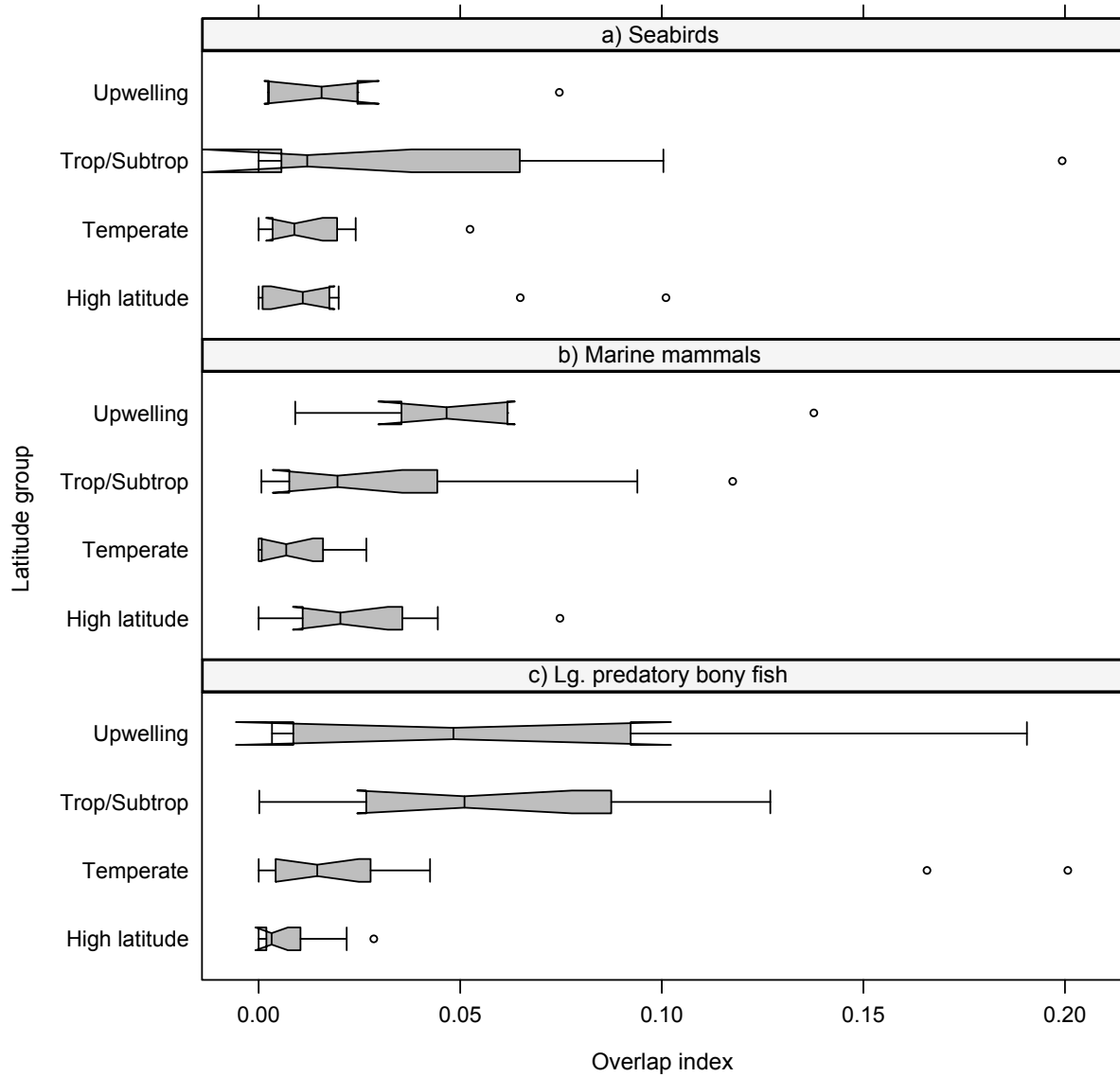
Figure 3.12 Notched box plots of trophic overlap index values between fisheries and a) seabirds, b) marine mammals, and c) large predatory bony fish across latitude groups. Lines inside box plots represent the median values, while the left and right segments represent the 0.25 and 0.75 quartiles respectively. Open circles represent data outliers identified by the R statistical software.
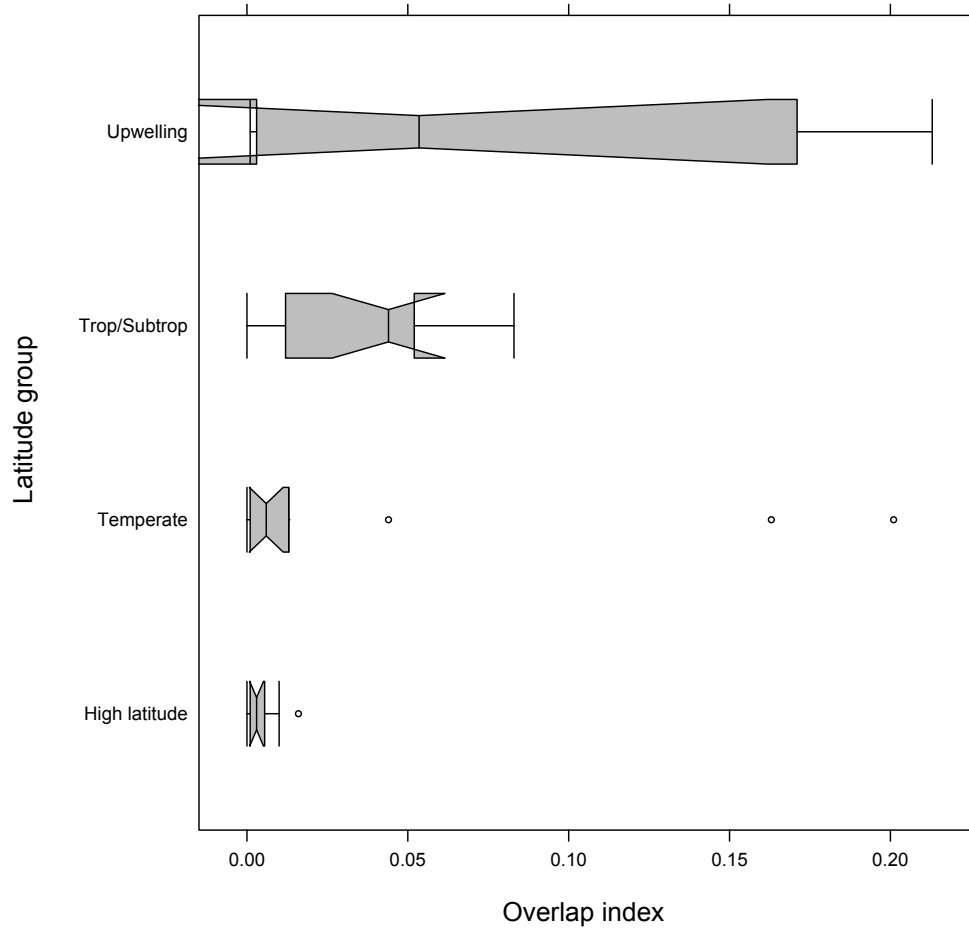
Figure 3.13 Notched box plots of trophic overlap index values between fisheries and all predators combined across latitude groups. Lines inside box plots represent the median values, while the left and right segments represent the 0.25 and 0.75 quartiles respectively. Open circles represent data outliers identified by the R statistical software.
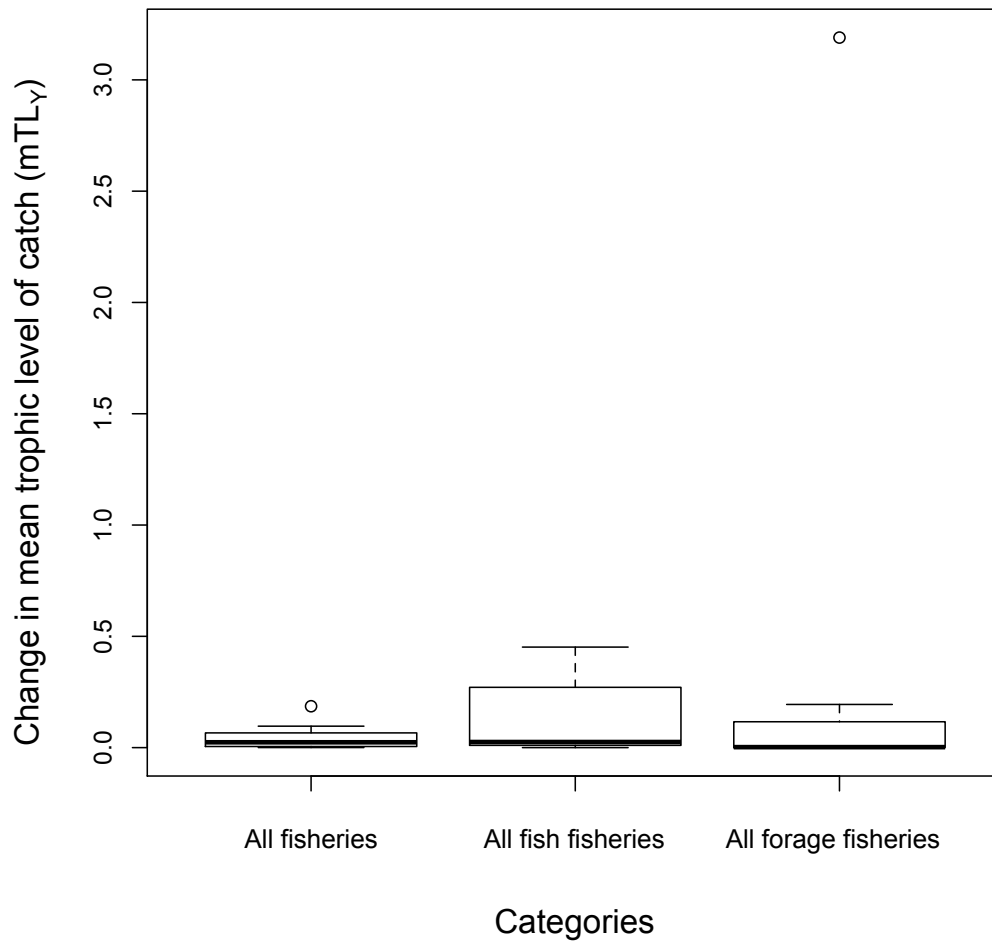
Figure 3.14 Box plots showing the change in *mTL*$_Y$ values from including and excluding discards for the 14 Ecopath models that had this data available (Table 3.1). Lines inside box plots represent the median values, while the lower and upper segments represent the 0.25 and 0.75 quartiles respectively. Open circles represent data outliers identified by the R statistical software.

3.6 Chapter 3 Tables

Table 3.1 List of all 43 Ecopath models used in this study. Approximate locations of Ecopath models can be found in Figure 3.1. LDO = landings data only. [1]48 group model, [2]pre-oil spill model, [3]post-oil spill model, [4]ETP7 model, [5]La Niña model, [6]El Niño model, [7]1990 model, [8]1995 model.

#	Model name	Latitude group	LDO	Discard data	Pedigree index	Citation
1	W. Bering Sea[1]	High latitude	No	Yes	-	(Aydin et al. 2002)
2	E. Bering Sea (1)	High latitude	No	Yes	-	(Trites et al. 1999)
3	E. Bering Sea (2)	High latitude	No	No	-	(Aydin et al. 2002)
4	Prince William Sound, Alaska[2]	High latitude	No	No	0.351	(Dalsgaard & Pauly 1997)
5	Prince William Sound, Alaska[3]	High latitude	No	Yes	0.675	(Okey & Pauly 1999)
6	Hecate Strait, N. British Columbia	Temperate	No	Yes	-	(Ainsworth et al. 2002)
7	N. California Current	Upwelling	No	No	-	(Field et al. 2006)
8	Gulf of California	Tropical/Subtropical	No	Yes	-	(Arreguín-Sánchez et al. 2002)
9	E. Subtropical Pacific Ocean[4]	Tropical/Subtropical	No	Yes	-	(Olson & Watters 2003)
10	Gulfo Dulce, Costa Rica	Tropical/Subtropical	No	No	-	(Wolff et al. 1996)
11	N. Humboldt Current[5]	Upwelling	No	No	0.638	(Tam et al. 2008)
12	N. Humboldt Current[6]	Upwelling	No	No	0.638	(Tam et al. 2008)
13	Sechura Bay, Peru	Upwelling	No	No	0.462	(Taylor et al. 2008)
14	Antarctic Peninsula	High latitude	No	No	-	(Erfan & Pitcher 2005)
15	S. Orkneys/S. Georgia	High latitude	No	No	-	(Bredesen 2004)

16	Falkland Islands	Temperate	No	No	-	(Cheung & Pitcher 2005)
17	N. Gulf of Mexico	Tropical/Subtropical	Yes	No	0.240	(Geers 2012)
18	W. Florida shelf	Tropical/Subtropical	No	No	-	(Okey et al. 2004)
19	Delaware Bay	Temperate	No	No	-	(Frisk et al. 2011)
20	Gulf of Maine	Temperate	No	Yes	-	(Heymans 2001)
21	N. Gulf of St. Lawrence	Temperate	No	Yes	0.651	(Morissette et al. 2003)
22	Newfoundland	Temperate	No	No	0.396	(Heymans & Pitcher 2002)
23	Lancaster Sound region, Canada	High latitude	Yes	No	-	(Mohammed 2001)
24	Barents Sea[7]	High latitude	No	No	-	(Blanchard et al. 2002)
25	Barents Sea[8]	High latitude	No	No	-	(Blanchard et al. 2002)
26	Icelandic shelf	High latitude	Yes	No	0.295	(Mendy 1999)
27	English Channel	Temperate	No	Yes	-	(Stanford & Pitcher 2004)
28	W. English Channel	Temperate	No	Yes	-	(Araújo et al. 2005)
29	N. & C. Adriatic Sea	Temperate	No	Yes	0.657	(Coll et al. 2007)
30	NW Mediterranean Sea	Temperate	No	No	-	(Coll et al. 2006)
31	Azores Archipelago	Temperate	No	No	0.409	(Guénette & Morato 2001)
32	Atlantic coast of Morocco	Upwelling	No	No	0.382	(Stanford et al. 2004)
33	Banc d'Arguin, Mauritanie	Tropical/Subtropical	Yes	No	0.537	(Sidi & Diop 2004)
34	Cape Verde Archipelago	Tropical/Subtropical	Yes	No	-	(Stobberup et al. 2004)
35	Central Atlantic Ocean	Temperate	Yes	No	-	(Vasconcellos & Watson 2004)

36	Gambian continental shelf	Tropical/Subtropical	No	Yes	-	(Mendy 2004)
37	Guinea-Bissau continental shelf	Tropical/Subtropical	No	Yes	-	(Amorim et al. 2004)
38	Senegambia	Tropical/Subtropical	Yes	No	-	(Samb & Mendy 2004)
39	Guinean continental shelf	Tropical/Subtropical	No	No	-	(Gascuel et al. 2009)
40	S. Benguela Current	Upwelling	Yes	No	-	(Shannon et al. 2003)
41	Kerguelen Archipelago EEZ	Temperate	No	No	-	(Pruvost et al. 2005)
42	Hong Kong, China	Tropical/Subtropical	No	Yes	-	(Buchary et al. 2002)
43	East China Sea	Tropical/Subtropical	No	No	0.636	(Jiang et al. 2008)

Table 3.2 Median predator production rates (t km^{-2} y^{-1}) across latitude groups with 95% confidence intervals (CI).

Predator category	Latitude group	Median	Lower 95% CI	Upper 95% CI
Seabird	Upwelling	0.0011	0.0004	0.08054
	Tropical/Subtropical	0.0016	0.0005	0.0072
	Temperate	0.0069	0.0040	0.1624
	High latitude	0.0077	0.0041	0.0932
Marine mammal	Upwelling	0.0127	0.0012	0.0848
	Tropical/Subtropical	0.003	0.0011	0.0163
	Temperate	0.0022	0.0012	0.0360
	High latitude	0.0197	0.0144	0.0314
Lg. predatory fish	Upwelling	2.0510	0.5581	9.4780
	Tropical/Subtropical	0.9363	0.2589	4.0324
	Temperate	0.4031	0.2581	2.6590
	High latitude	1.9946	1.3275	16.6455

Table 3.3 Median predator production rates supported by forage fish (t km^{-2} y^{-1}) across latitude groups with 95% confidence intervals (CI).

Predator category	Latitude group	Median	Lower 95% CI	Upper 95% CI
Seabird	Upwelling	0.0010	0.0002	0.5235
	Tropical/Subtropical	0.0010	0.0006	0.0049
	Temperate	0.0025	0.0017	0.0917
	High latitude	0.0041	0.0012	0.0461
Marine mammal	Upwelling	0.0037	0.0001	0.0260
	Tropical/Subtropical	0.0003	0.0002	0.0057
	Temperate	0.0003	0.0002	0.0127
	High latitude	0.0058	0.0029	0.0146
Lg. predatory fish	Upwelling	0.6024	0.1191	5.0426
	Tropical/Subtropical	0.1579	0.0603	0.7410
	Temperate	0.1560	0.0804	0.3537
	High latitude	0.6777	0.3699	1.3680

Table 3.4 Summary of coefficients of determination (r^2) and level of statistical significance for linear regression models between the proportion of fish biomass (including cephalopods) consisting of forage fish and the proportion of forage fish in a predator's diet analyzed for each predator category in every latitude group. N = number of ecosystem models and ns = not statistically significant (p > 0.05). [1]p values ≤ 0.05 were considered statistially significant.

Predator category	N	Latitude group	r^2	p value[1]
Seabird	6	Upwelling	0.40	ns
	12	Tropical/Subtropical	0.05	ns
	14	Temperate	0.17	ns
	11	High latitude	0.49	0.016
Marine mammal	6	Upwelling	0.49	ns
	11	Tropical/Subtropical	0.06	ns
	14	Temperate	0.12	ns
	10	High latitude	0.73	0.002
Lg. predatory fish	5	Upwelling	0.43	ns
	10	Tropical/Subtropical	0.13	ns
	14	Temperate	0.44	0.01
	10	High latitude	0.34	ns

Chapter 4. Toxicity of the harmful dinoflagellate, Cochlodinium polykrikoides, to early life stages of three estuarine forage fish species

A version of this Chapter is in review for publication in Marine Ecology Progress Series: Rountos, K.J., Tang, Y-Z., Cerrato, R.M., Gobler, C.J., and Pikitch, E.K. (in press) Toxicity of the harmful dinoflagellate, *Cochlodinium polykrikoides*, to early life stages of three estuarine forage fish.

4.1 Introduction

Harmful algal blooms (HABs) are caused by a variety of marine phytoplankton species, many of which produce potent biotoxins (Landsberg 2002). HABs can be ecologically and economically destructive, causing mass mortalities in both wild and farmed fish and shellfish species globally (Shumway 1990, Whyte et al. 2001, Lee et al. 2002, Imai et al. 2006, Anton et al. 2008, Gobler et al. 2008, Richlen et al. 2010). While these impacts are substantial, little is known about the broader ecological impacts of many HABs (Smayda 1991, Landsberg 2002, Kudela & Gobler 2012). Forage fish play a crucial role in marine ecosystems by feeding on algae and other plankton and transferring energy to upper trophic levels (Pikitch et al. 2012), and may be particularly susceptible to HABs. Thus impacts to this group of fishes may have cascading effects within aquatic food webs, as well as important economic consequences (Pikitch et al. 2014).

Blooms of the toxic dinoflagellate *Cochlodinium polykrikoides* have increased in geographic extent, frequency, and duration in many coastal ecosystems worldwide (Kudela & Gobler 2012). In many regions of Asia, Europe and North America, these blooms are now annual events (Lee et al. 2002, Gobler et al. 2008, Tomas & Smayda 2008, Richlen et al. 2010, Kudela & Gobler 2012), presenting significant challenges to the management and conservation of coastal living resources (Landsberg 2002, Anderson 2009, Kim 2010).

Much of our current understanding of the ichthyotoxicity of *C. polykrikoides* and other HABs is based on traditional laboratory controlled experiments or field observations using mostly larval, juvenile or adult fish (Onoue et al. 1985, Kim et al. 1999, Landsberg 2002, Gobler et al. 2008, Tang & Gobler 2009). While studies on these life stages have been useful in determining the toxicity of *C. polykrikoides*, more research is needed to identify the causative agents of *C. polykrikoides* toxicity (Kim et al. 1999, Tang & Gobler 2009, Kudela & Gobler 2012). In addition, no study to date has evaluated the toxicity of *C. polykrikoides* to early life stages (ELS) of fish (i.e. embryos and eleutheroembryos). Toxicity to ELS fish could be ecologically significant, but may go unnoticed in the wild because of their relatively small size (Tang & Gobler 2009). Impacts to ELS fish may affect the recruitment of fish populations (Houde 1989, Rothschild 2000, Houde 2008), the productivity of fisheries, upper trophic level predators, and food web dynamics (Rothschild 2000, Pikitch et al. 2012).

The use of ELS fish bioassays for HAB toxicology research has been very limited, both in terms of the algae and the model organisms investigated. Only three fish species, the Japanese medaka (*Oryzias latipes*)(Kimm-Brinson & Ramsdell 2001), the zebrafish (*Danio rerio*)(Lefebvre et al. 2004, Berry et al. 2007) and the red drum (*Sciaenops ocellatus*)(Riley et al. 1989) have been used in studies conducted to date. Of these, red drum was the only species that was gathered from the wild and not produced from a hatchery (Riley et al. 1989).

In this study, the toxicity of *C. polykrikoides* to ELS's of three species of forage fish common to U.S. East Coast estuaries was assessed. It was demonstrated that *C. polykrikoides* caused significant mortality to newly hatched eleutheroembryos of these species but generally not to embryos. In addition, it was found that short-term exposure to *C. polykrikoides* inhibited the motility of eleutheroembryos, although this may be regained depending on the exposure time and the fish species. This research furthers understanding of the potential ecosystem effects of *C. polykrikoides* blooms, and underscores the importance and utility of incorporating ELS fish in future toxicology studies with HABs.

4.2 Material and Methods
4.2.1 *Cochlodinium polykrikoides* clonal culture

The dinoflagellate *C. polykrikoides* (strain CP1) was isolated from bloom water collected in Flanders Bay, Peconic Estuary, New York, USA in 2006 (Tang & Gobler 2009). Clonal culture of *C. polykrikoides* was maintained in sterile GSe culture medium prepared according to Tang & Gobler (2009). Briefly, the culture medium was prepared with autoclaved and filtered (0.22 μm) coastal Atlantic Ocean seawater (Salinity: 30) supplemented with stock nutrients and an antibiotics solution (a mixture of 10,000 I.U. penicillin and 10,000 μg ml^{-1} streptomycin, Mediatech. Inc., Hemdon, VA, USA) with a final concentration of 2% (Tang & Gobler 2009). Cultures of *C. polykrikoides* were incubated at 21°C following a 12 h light: 12 h dark photoperiod with a light intensity ~100 μmol quanta m^{-2} s^{-1} (Tang & Gobler 2009). Batches of *C. polykrikoides* clonal cultures were generally within early exponential growth phases when they were used for experiments, as cells in this phase are most physiologically active (Tang & Gobler 2009).

4.2.2 Fish collection and selection

All procedures used were approved by the Institutional Animal Care and Use Committee at Stony Brook University (Stony Brook, NY, USA) for fish collection, handling, experimental design, and disposal, using organisms approved for toxicity research (EPA 2002). Atlantic silversides (*Menidia menidia*) embryos were obtained from either strip spawning adult fish collected by beach seine from Shinnecock Bay, NY, USA (Temperature: 21-23°C, Salinity: 28-30) using methods described in Costello et al. (1957) or by natural photoperiod-induced spawning of a separate F1 population of fish maintained at Flax Pond Laboratory, Stony Brook, NY, USA (Temperature: 24°C, Salinity 25). Inland silversides (*Menidia beryllina*) were obtained from hatchery stocks maintained by Aquatic Resource Organisms (Hampton, NH, USA) (Temperature 25°C, Salinity 25-30), while sheepshead minnow (*Cyprinodon variegatus*) embryos were obtained from Aquatic Bio Systems (Fort Collins, CO, USA) (Temperature 20-25°C, Salinity 25-30).

Embryos used in experiments were <24 hours old post fertilization (hpf), which allowed for differentiation between successfully fertilized embryos with healthy appearances (i.e. translucent yellow color) from those that were unfertilized or dead (i.e. opaque white color (EPA 1996)). Prior to all experiments, embryos were selected using flexible forceps, counted and placed into sterilized nutrient ameliorated culture media for at least two hours. This was done to wash any residues from the embryos and allow them to acclimate. Culture medium served as a control treatment in our experiments (Tang & Gobler 2009). Rinsed embryos were then visually inspected under an inverted light microscope (Nikon Eclipse TS100, Nikon, USA) at 40x to confirm that sufficient numbers of healthy, fertilized embryos were available for experiments.

Eleutheroembryos, defined as newly hatched fish that are still feeding on their yolk sac (Belanger et al. 2010, Embry et al. 2010), for all three species were obtained by hatching embryos. Embryos used for hatching were placed into separate 1 l beakers filled with filtered (0.2 μm) and UV sterilized seawater (Salinity: 30). Beakers received constant bubble aeration and followed an approximate photoperiod of 12 h light: 12 h dark at ~25°C. Beakers were periodically checked for hatching over several days, depending on the species, and water exchanges (0.5 l) occurred every 2-3 days. Eleutheroembryos used in experiments were <24 hours old post hatch (hph) for all species. Once hatched, eleutheroembryos were counted and transferred into sterilized nutrient ameliorated culture media (Salinity: 30) using a modified transfer pipette (Samco Scientific Co., San Fernando, CA, USA). Eleutheroembryos were acclimated for at least two hours in fresh sterile medium before experiments.

4.2.3 Embryo toxicity experiments (Experiments 1-3)

Embryo experiments were conducted using 24-well polystyrene cell culture plates. All experiments included a culture medium control (0 cells ml^{-1}) and an undiluted *C. polykrikoides* clonal culture treatment (3 - 6 x 10^3 cells ml^{-1}) (Table 4.1). Cell densities of undiluted *C. polykrikoides* clonal cultures were similar to those documented in natural *C. polykrikoides* blooms (Gobler et al. 2008). Depending on the experiment, several intermediary *C. polykrikoides* treatments were prepared by diluting *C. polykrikoides*

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clonal culture with culture medium (Table 4.1). All dilution treatments in each experiment were prepared in the same flask, starting with the control treatment and increasing in *C. polykrikoides* cell density. Dilution treatments were dispensed into replicate wells (3 ml in each well). Acclimated embryos were then haphazardly selected and allocated into plate wells in a sequential manner starting with the first replicate (well) on each treatment plate, before proceeding to other wells in a treatment plate. This process was repeated until all replicates in plates had an embryo to reduce any potential selection bias across treatment plates. After allocation of embryos, an inverted light microscope was used to confirm that each well had an embryo and a digital image was captured (Nikon Insight camera, Nikon, USA) to assess the size of embryos. Dilution treatments, fish per treatment, and total sample sizes for all ELS experiments are shown in Table 4.1. All embryos were exposed to *C. polykrikoides* treatments continuously throughout their embryonic development (i.e. 5-8 d depending on the fish species) and the remaining duration of the experiments (Table 4.1). Embryos were microscopically examined periodically (Table 4.1) throughout the duration of experiments and mortality and hatching was assessed. Post-hatch mortality was recorded and analyzed in Experiments 1 and 2 but this was not possible for Experiment 3.

4.2.4 Eleutheroembryo experiments

To determine the toxicity of *C. polykrikoides* to eleutheroembryos, two types of experiments were conducted: 1) 2 d static exposure experiments to assess the acute toxicity of *C. polykrikoides* clonal culture, and 2) exposure/recovery experiments to evaluate lethal and sublethal toxicity of short-term exposure of eleutheroembryos to *C. polykrikoides* culture. Both experiment types were conducted using multiple 24-well polystyrene plates and utilized eleutheroembryos (<24 hph) for each respective fish species. Calibrated digital images of eleutheroembryos were taken at either time of death or experimental termination for length measurements using NIS-Elements BRTM Imaging (Build 728) software 3.22.11 (LO, Nikon).

4.2.4.1 Eleutheroembryo acute toxicity experiments (Experiments 4-6)

For 2 d static acute toxicity experiments, dilutions of *C. polykrikoides* culture were prepared in the same manner as embryo experiments and at similar cell densities (0 to 8 x 10^3 cells ml^{-1}) (Table 4.1). Mortality was assessed every 24 h by visual inspection under an inverted light microscope. An eleutheroembryo was considered dead if there was no sign of a heartbeat after 20 seconds of inspection (EPA 1996).

4.2.4.2 Exposure/recovery experiments (Experiments 7-9)

Given the heterogeneous nature of *C. polykrikoides* blooms (Kudela & Gobler 2012), exposure/recovery experiments were designed to assess how short-term exposures (i.e. swimming in) to a bloom "patch" may impact fish. Exposure/recovery experiments followed a randomized block design using 24-well plates, in which each plate contained one replicate of each treatment. Experiments varied in both *C. polykrikoides* cell densities (i.e. undiluted *C. polykrikoides*, 50% diluted *C. polykrikoides* and control) and exposure time (Table 4.1). In these experiments, a treatment replicate consisted of two wells on a given plate, an exposure well and a recovery well. Following the exposure period, all eleutheroembryos were transferred to an adjacent recovery well, which contained either *C. polykrikoides* at the same cell density or culture medium (control). Eleutheroembryos whose exposure well contained culture medium (0 cells ml^{-1}) were transferred to recovery wells containing culture medium (0 cells ml^{-1}) to account for the potential effects of pipetting and transferring on fish. Treatments in which eleutheroembryos were transferred to control recovery wells after *C. polykrikoides* exposure will be referred to as "partial" exposure treatments, while those transferred to the same *C. polykrikoides* treatments will be referred to as "full" exposure treatments henceforth. Eleutheroembryos remained in recovery wells for the duration of these experiments and were periodically checked for viability (Experiments: 7,8,9) and motility (Experiment 9) (Table 4.1).

4.2.4.2.1 Experiment 7 (*Menidia menidia*)

Eleutheroembryos in partial exposure treatments were exposed to undiluted *C. polykrikoides* (4 x10^3 cells ml^{-1}) or 50% diluted *C. polykrikoides* (2 x10^3 cells ml^{-1}) for either 0.5 or 0.75 h before being transferred into recovery wells containing control culture

medium (0 cells ml^{-1}). Full exposure treatments were transferred to recovery wells that contained identical *C. polykrikoides* cell densities following the same exposure times. Eleutheroembryos in all treatments were monitored for 2 days.

4.2.4.2.2 Experiment 8 (*Menidia beryllina* and *Cyprinodon variegatus*)

Eleutheroembryos of two fish species (*M. beryllina* and *C. variegatus*) were exposed to three concentrations of *C. polykrikoides*; undiluted (6 x 10^3 cells ml^{-1}), 50% diluted (3 x 10^3 cells ml^{-1}) and control (0 cells ml^{-1}). Eleutheroembryos were transferred into recovery wells after 0.25 h in exposure wells. Eleutheroembryo mortality was monitored for 2.75 days.

4.2.4.2.3 Experiment 9 (*Cyprinodon variegatus*)

Because *C. variegatus* eleutheroembryos exposed to *C. polykrikoides* displayed the highest survival among the three species investigated, the effects of this alga on the swimming abilities of this fish species were investigated. Eleutheroembryos in partial exposure treatments were exposed to undiluted *C. polykrikoides* cultures (6 x 10^3 cells ml^{-1}) for 1, 1.75, 2.5 or 3.5 h before being transferred to control recovery wells. Full exposure treatments were transferred to recovery wells of similar *C. polykrikoides* densities following these same exposure times. Eleutheroembryo mortality and motility were monitored for 4 days periodically throughout the experiment (Table 4.1). Eleutheroembryo motility was classified as "swimming" or "not swimming", depending on whether the fish propelled itself in any direction after 20 seconds of observation at each check point throughout the experiment (Table 4.1). Time to swimming inhibition, the maximum time immobilized and time to swimming recovery were calculated for each eleutheroembryo. Time to swimming inhibition was defined as the time period from the beginning of the experiment until the eleutheroembryo was first classified as "not swimming". Maximum time immobilized was defined as the longest time period that an eleutheroembryo was consecutively classified as "not swimming", and time to swimming recovery was the time period required for a previously "not swimming" eleutheroembryo to be consistently classified as "swimming".

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4.2.5 Statistical analyses

Data collected from all experiments were analyzed using the R statistical software (CRAN R, version 2.15.0, www.R-project.org/) with a time to event package (package survival). Specifically, time to death of embryos or eleutheroembryos and time to hatch of embryos were analyzed by survival analysis with censoring. Censoring allowed for individuals surviving or hatching beyond the experiment end to be included in our analyses. Several parametric hazard distributions were evaluated and ultimately the Weibull distribution was used because it generally provided the best fit to experimental data. Embryo experiments evaluated time to death and time to hatch of embryos primarily, but time to death for hatched eleutheroembryos was also analyzed when possible. Because of heterogeneity of variance in Experiments 7, 8 and 9, likely due to a large number of treatments with zero or 100% survival, treatments were compared using pairwise t-tests with Bonferroni adjusted error rates. This adjustment procedure is considered conservative and reduces Type-one error (Sokal & Rohlf 1995, McDonald 2009). Eleutheroembryo experiments evaluated time to death as well as sublethal effects to motility (Experiment 9). Time to swimming inhibition, total time immobilized, and time to swimming recovery, were also analyzed using a pairwise t-test with Bonferroni adjusted error rates. To account for the influence of eleutheroembryos dying during the experiment, motility data were analyzed by excluding dead individuals entirely from the analysis. All experiments with multiple *C. polykrikoides* dilution treatments were analyzed as a continuous factor, since they covered a wide range of cell densities, from 0 cells ml^{-1} to bloom concentrations (Table 4.1).

4.3 Results
4.3.1 Embryo toxicity experiments (Experiments 1-3)

4.3.1.1 Time to embryo death

Embryo survival for *M. menidia* across all treatments (Experiment 1) was high (>90%) and time to embryo death was not significantly different between control and *Cochlodinium polykrikoides* treatments (Table 4.2). Survival of *M. beryllina* embryos (Experiment 2) was >81% for the control and lower dilutions of *C. polykrikoides* and

only 4% (1 out of 23 embryos) when embryos were exposed to 5×10^3 *C. polykrikoides* cells ml^{-1}. Survival of embryos exposed to lower doses of *C. polykrikoides* did not differ from controls and time to death of *M. beryllina* embryos was not significantly different between controls and *C. polykrikoides* treatments (Table 4.2). Survival of *C. variegatus* embryos (Experiment 3) in control and lower *C. polykrikoides* cell densities ranged from 80% to 100%, while exposure to the high densities of *C. polykrikoides* (6.4×10^3 cell ml^{-1}) reduced survival to 46% (6 out of 13 embryos). Time to embryo death, however, was not significantly different between controls and *C. polykrikoides* treatments (Table 4.2).

4.3.1.2 Time to hatch

Hatching success across all treatments in Experiment 1 (*M. menidia*) was ≥91%. Embryos in control treatments hatched significantly later than embryos in *C. polykrikoides* treatments (p < 0.0001, Table 4.2). Hatching success of *M. beryllina* (Experiment 2) was 4% at 5×10^3 *C. polykrikoides* cells ml^{-1} and >81% in all other treatments. Time to hatch in *C. polykrikoides* treatments also occurred significantly later for *M. beryllina* embryos compared to controls (p = 0.0007, Table 4.2). No statistically significant differences in time to hatch or hatching success were found for *C. variegatus* embryos in Experiment 3 (Table 4.2).

4.3.1.3 Time to eleutheroembryo death

Time to death of eleutheroembryos in *C. polykrikoides* treatments occurred significantly earlier than in control treatments for *M. menidia* and *M. beryllina* eleutheroembryos (p = 0 and p < 0.0001 respectively, Table 4.2). Survival of *M. menidia* eleutheroembryos (Experiment 1) was >85% for all *C. polykrikoides* treatments ≤7.6 x 10^2 cells ml^{-1}, but was ≤5% for treatments with >7.6 x 10^2 *C. polykrikoides* cells ml^{-1}. Survival of *M. beryllina* eleutheroembryos (Experiment 2) ranged from 41% to 90% in *C. polykrikoides* treatments ≤4.9 x 10^2 cells ml^{-1} and the control. No *M. beryllina* eleutheroembryos survived in *C. polykrikoides* treatments ≥1.2 x 10^3 cells ml^{-1}. Survival of *C. variegatus* eleutheroembryos (Experiment 3) was ≥89% in all treatments.

4.3.2 Eleutheroembryo experiments

4.3.2.1 Eleutheroembryo acute toxicity experiments (Experiments 4-6)

Eleutheroembryos of all fish species exposed to high densities of *C. polykrikoides* experienced complete mortality during the first day of post-hatch exposure (Figure 4.1). Survival in lower *C. polykrikoides* cell density treatments varied by fish species and *C. polykrikoides* cell density. All *C. variegatus* in experiment 6 survived *C. polykrikoides* treatments with densities ≤1.6 x 10^3 cells ml^{-1}, while *M. menidia* (Experiment 4) and *M. beryllina* (Experiment 5) had high survival, >75 and 100% respectively, in *C. polykrikoides* treatments ≤4.0-5.0 x 10^2 cells ml^{-1} (Figure 4.1). Survival analyses revealed that time to eleutheroembryo death decreased significantly with increasing *C. polykrikoides* cell densities in all these experiments (p = 0 for experiments 4-6, Table 4.2).

4.3.2.2 Eleutheroembryo exposure/recovery experiments (Experiments 7-9)

4.3.2.2.1 Experiment 7 (*Menidia menidia*)

Time to eleutheroembryo death occurred significantly earlier (p < 0.0001) in full exposure (i.e. 3.7 x 10^3 cells ml^{-1} : 3.7 x 10^3 cells ml^{-1}, 1.9 x 10^3 cells ml^{-1} : 1.9 x 10^3 cells ml^{-1}) and the high cell density (3.7 x 10^3 cells ml^{-1} : 0 cells ml^{-1}) partial exposure treatments compared to the control (0 cells ml^{-1} : 0 cells ml^{-1}) and the lower cell density (1.9 x 10^3 cells ml^{-1} : 0 cells ml^{-1}) partial exposure treatments at both exposure times tested (i.e. 0.5 and 0.75 h) (Table 4.3, Figure 4.2). Eleutheroembryos in lower cell density partial exposure (1.9 x 10^3 cells ml^{-1} : 0 cells ml^{-1}) treatments had greater survival (i.e. 0.5 h = 67%, 0.75 h = 83%) than full exposure (1.9 x 10^3 cells ml^{-1} : 1.9 x 10^3 cells ml^{-1}) treatments (i.e. 0% for both exposure times). In contrast, no significant differences in time to eleutheroembryo death were found between partial (1.9 x 10^3 cells ml^{-1} : 0 cells ml^{-1}) and control (0 cells ml^{-1} : 0 cells ml^{-1}) treatments (Table 4.3). Finally, a 0.5 h exposure to 3.7 x 10^3 *C. polykrikoides* cells ml^{-1} was enough to cause 83% mortality after just 1 h and complete mortality after 2.7 h in the high cell density partial exposure (3.7 x 10^3 cells ml^{-1} : 0 cells ml^{-1}) treatment (Figure 4.2a).

4.3.2.2.2 Experiment 8 (*Menidia beryllina* and *Cyprinodon variegatus*)

There were differences in the survival of *M. beryllina* and *C. variegatus* eleutheroembryos after a 0.25 h exposure to similar *C. polykrikoides* cell densities (Figure 4.3). Survival analyses across all treatments for *M. beryllina* and *C. variegatus* revealed that time to eleutheroembryo death only occurred significantly earlier in the high cell density full exposure (6.0×10^3 cells ml^{-1} : 6.0×10^3 cells ml^{-1}) *C. polykrikoides* treatments compared to the controls ($p = 0.005$ and $p < 0.0001$ respectively, Table 4.3). Survival of *M. beryllina* in the lower cell density (3.0×10^3 cells ml^{-1} : 0 cells ml^{-1}) partial exposure treatment was high (82%), and nearly identical to the control (0 cells ml^{-1} : 0 cells ml^{-1}), while survival in the full exposure treatment (3.0×10^3 cells ml^{-1} : 3.0×10^3 cells ml^{-1}) was only 10% (Figure 4.3a). Similarly, survival in the high cell density (6.0×10^3 cells ml^{-1} : 0 cells ml^{-1}) partial exposure treatments was higher (30%) than the high cell density full exposure (6.0×10^3 cells ml^{-1} : 6.0×10^3 cells ml^{-1}) treatment (0%) for *M. beryllina*. Complete survival of *C. variegatus* eleutheroembryos was found in all treatments except for the high cell density *C. polykrikoides* full exposure (6.0×10^3 cells ml^{-1} : 6.0×10^3 cells ml^{-1}) treatment, where it was 10% (Figure 4.3b).

4.3.2.2.3 Experiment 9 (*Cyprinodon variegatus*)

Survival in the partial exposure (6.2×10^3 cells ml^{-1} : 0 cells ml^{-1}) treatments was >82% at exposure times ≤2.5 h and 55% in the 3.5 h exposure treatment, while no eleutheroembryos survived in any of the high cell density full exposure treatments (Figure 4.4). Time to death occurred significantly earlier, in about 2.73 to 3.75 days, in full exposure (6.2×10^3 cells ml^{-1} : 6.2×10^3 cells ml^{-1}) *C. polykrikoides* treatments compared to control (0 cells ml^{-1} : 0 cells ml^{-1}) and partial exposure (6.2×10^3 cells ml^{-1} : 0 cells ml^{-1}) treatments ($p < 0.0001$ for all exposure times ; Table 4.3). Time to eleutheroembryo death in partial (6.2×10^3 cells ml^{-1} : 0 cells ml^{-1}) exposure treatments only occurred significantly earlier (~2.42 d) than control (0 cells ml^{-1} : 0 cells ml^{-1}) treatments following a 3.5 h exposure to *C. polykrikoides* ($p < 0.05$, Table 4.3).

Exposures to *C. polykrikoides* caused swimming to be inhibited within 3.5 h for all eleutheroembryos in full (6.2×10^3 cells ml^{-1} : 6.2×10^3 cells ml^{-1}) and 96% of fish in partial (6.2×10^3 cells ml^{-1} : 0 cells ml^{-1}) exposure treatments. Time to swimming

inhibition occurred significantly earlier in these exposure treatments compared to controls (0 cells ml^{-1} : 0 cells ml^{-1}) (Table 4.4), where swimming was inhibited in only 7% of eleutheroembryos. Immobilized individuals in controls however began to swim again in less than 1 h and remained swimming for the remainder of the experiment. All eleutheroembryos in full exposure treatments died by the end of the experiment while only 18% of eleutheroembryos perished in partial exposure *C. polykrikoides* treatments (Table 4.4). As such, motility data was analyzed by excluding dead individuals from all analyses. Eleutheroembryo motility in partial exposure treatments varied with exposure times, with longer *C. polykrikoides* exposure times generally leading to increased immobilization and swimming recovery times (Figure 4.5). Total immobilization times in partial exposure treatments were significantly greater than controls at 1.75 h ($p < 0.005$), 2.5 h ($p < 0.0001$) and 3.5 h ($p < 0.0001$) exposure times when dead individuals were excluded from the analysis (Table 4.4). A similarly significant pattern emerged for swimming recovery times between controls and partial exposure treatments (Table 4.4). Eleutheroembryos in the 3.5 h partial exposure treatment had significantly longer recovery times (median: 36.75 h) than fish exposed to high levels of *C. polykrikoides* for 1 h (median: 6 h, $p < 0.0001$), 1.75 h (median: 6 h, $p < 0.0001$) but not 2.5 h (median: 30.5 h) (Table 4.4, Figure 4.5).

4.4 Discussion

4.4.1 Effects of *Cochlodinium polykrikoides* to early life stage fish in an ecosystem context

Blooms of *C. polykrikoides* often occur in high density (10^3-10^5 cells ml^{-1}) patches which can persist for many months and cover large coastal areas (>1 km^2) throughout the world (Onoue et al. 1985, Anton et al. 2008, Gobler et al. 2008, Richlen et al. 2010). It is thus likely that these blooms overlap with multiple life history stages of coastal fish populations, especially when blooms last for periods greater than 8 months (Richlen et al. 2010) or occur during seasons of high coastal fish activity in temperate latitudes (Gobler et al. 2008). Tang & Gobler (2009) hypothesized that *C. polykrikoides* blooms may cause cryptic mortality of smaller life stages of fish. This study confirms that

newly hatched eleutheroembryos of several forage fish species common to the U.S. East Coast can experience rapid mortality and sublethal effects to motility when exposed to *C. polykrikoides*. Although *C. polykrikoides* cultures have been found to be more toxic than bloom water at equivalent cell densities (Tang & Gobler 2009), similar toxicological responses are observed at higher bloom water concentrations ($\geq 10^4$), which are commonly found in natural bloom patches (Gobler et al. 2008, Tang & Gobler 2009).

M. menidia and *M. beryllina* species were more sensitive to *C. polykrikoides* than *C. variegatus*, and eleutheroembryos were more sensitive than the embryo life stage. In general, survival was relatively high in embryos exposed to *C. polykrikoides* treatments until they hatched, suggesting that the toxic agents in *C. polykrikoides* do not easily penetrate the chorionic membrane of these species, similar to a variety of other toxicants (Riley et al. 1989, Lammer et al. 2009, Embry et al. 2010). However, in the *M. beryllina* embryo experiment (Experiment 2), survival of embryos was greatly reduced when exposed to an elevated cell density of *C. polykrikoides* (5×10^3 cells ml^{-1}), suggesting that mortality of embryos does occur at higher cell densities and/or longer exposures. The effects of *C. polykrikoides* exposure on embryo hatch times were less evident and contrasting. Although statistically significant differences were found between treatments for *M. menidia* and *M. beryllina*, they are likely not ecologically significant, because fertilization times could have naturally ranged by as much as ±5-7 h in these experiments. In addition, no significant differences in time to hatch were found in the *C. varieagatus* embryo experiment. Based on these results and the heterogeneous and episodic nature of *C. polykrikoides* blooms, it is unlikely that they pose an acute threat to wild fish embryos, at least until they hatch. However, there is increasing evidence that embryonic exposures to some toxicants can have delayed consequences that only become manifested in older life stages of fish (Weis & Weis 1995a, b, Timme-Laragy et al. 2006, Levin et al. 2011). These types of effects should be evaluated in future embryo toxicity experiments with this HAB.

Static acute toxicity experiments revealed rapid (<24 h) mortality of eleutheroembryos in all three fish species when exposed to the high *C. polykrikoides* cell

density treatments (2-7.9 x 10^3 cells ml^{-1}), which are typical of dense blooms (Kudela & Gobler 2012). The *C. polykrikoides* cell densities at which the greatest mortality occurred varied by fish species (Figure 4.1). Complete mortality occurred after exposure to 2.4 x 10^3 cells ml^{-1} for *M. menidia*, while similar depressed survival occurred at lower (7.9 x 10^2 cells ml^{-1}) and higher (4.8 x 10^3 cells ml^{-1}) *C. polykrikoides* cell densities for *M. beryllina* and *C. variegatus* respectively (Figure 4.1). These results demonstrate that individual fish species may have different sensitivities to *C. polykrikoides*.

While static acute toxicity experiments are valuable for determining baseline toxicology data, they are often difficult to interpret in an ecological context (Kimball & Levin 1985, de Vlaming & Norberg-King 1999). Exposures of marine organisms to HABs are likely not static in the natural environment, as exposure is influenced by a variety of factors, including water circulation and the potential motility of both target and HAB species (Landsberg 2002). *C. polykrikoides* blooms in particular can form large heterogeneous blooms that can persist for many months (Gobler et al. 2008, Richlen et al. 2010, Kudela & Gobler 2012). As such, the effects of relatively short-term (i.e. minutes to hours) *C. polykrikoides* exposures to eleutheroembryos were examined using critical exposure times and cell densities found in this and previous static acute toxicity studies that are ecologically relevant (Gobler et al. 2008, Tang & Gobler 2009). In general, exposure/recovery experiments demonstrated that both exposure to higher *C. polykrikoides* cell densities and longer exposure times significantly influenced the survival and time to death of eleutheroembryos for all species examined. Short-term (i.e. 0.5 and 0.75 h) exposures to *C. polykrikoides* (3.7 x 10^3 cells ml^{-1}) treatments caused >50% mortality to *M. menidia* eleutheroembryos within 1 h of exposure and >90% mortality at 2 days, regardless of whether fish were transferred to control (0 cells ml^{-1}) conditions after exposure. At lower *C. polykrikoides* cell densities in partial exposure (1.9 x 10^3 cells ml^{-1} : 0 cells ml^{-1}) treatments, eleutheroembryos exhibited high survival similar to controls (0 cells ml^{-1} : 0 cells ml^{-1}) (Figure 4.2). A similar result in the survival of *M. beryllina* eleutheroembryos was found when examining a shorter exposure time (0.25 h) to higher *C. polykrikoides* cell densities (Figure 4.3a). These results demonstrate that in an ecosystem setting, fish exposed to high levels of *C. polykrikoides* (>10^3 cells

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ml^{-1}) for a brief period of time that are subsequently exposed to very low levels - a potentially common occurrence given the heterogeneous nature of these blooms - are more likely to survive than individuals chronically exposed to high levels. As such, the impacts of *C. polykrikoides* to fish may be less severe than previously predicted by chronic exposure experiments (e.g. Tang & Gobler 2009).

Even though short-term exposures to *C. polykrikoides* may not necessarily be lethal, important sublethal effects were found in this study. The loss of swimming ability in *C. variegatus* eleutheroembryos is the first evidence of behavioral impacts from *C. polykrikoides* toxicity to fish. Behavioral information is especially valuable in understanding the broader ecological impacts of many toxicants (Little & Finger 1990), particularly in early life stage fish (Sloman & McNeil 2012). Negative impacts on swimming ability can have potentially large consequences for the survival of eleutheroembryos in coastal ecosystems, including the inability to escape predators or capture prey items (Weis & Weis 1995a, Zhou & Weis 1998, Samson et al. 2008, Sloman & McNeil 2012). The results from this study suggest that short-term exposures of eleutheroembryos to *C. polykrikoides* blooms could render exposed fish vulnerable, as they are incapacitated well before death actually occurs and do not recover their swimming ability for hours after exposure. In this regard, *C. polykrikoides* blooms may significantly impact the recruitment of coastal fish species, their distributions, and even food web dynamics, particularly when these bloom events coincide with reproductive events of fish. Further research however is still clearly needed to fully understand the ecosystem effects of this HAB species.

4.4.2 Use of ELS fish bioassay in future HAB toxicology research

Early life stage fish bioassays are now commonly used across many disciplines of toxicology (Berry et al. 2007, Lammer et al. 2009, Embry et al. 2010). Although ELS fish tests are regarded as comparable and effective alternatives to traditional acute toxicological experiments (Dave 1993, Braunbeck et al. 2005, Wedekind et al. 2007, Lammer et al. 2009, Embry et al. 2010), their use in HAB toxicology research has been relatively limited (Riley et al. 1989, Kimm-Brinson & Ramsdell 2001, Lefebvre et al.

2004, Berry et al. 2007). This study demonstrated that ELS fish can be effectively incorporated in toxicology research with *C. polykrikoides* and likely other HABs. The results of acute toxicity experiments using eleutheroembryos were similar to those using older life stage fishes, including larvae, juveniles and adults (Kim et al. 1999, Gobler et al. 2008, Tang & Gobler 2009). These findings suggest that future toxicology research with *C. polykrikoides* could utilize ELS *M. menidia*, *M. beryllina*, and *C. variegatus* instead of older conspecifics to achieve similar objectives. Using ELS fish also provides benefits compared to traditional bioassays with older life stages, including reduced research time and expenses, and may allow for a broader range of potential species to be examined (Dave 1993). For instance, it may be impractical or impossible to evaluate juvenile or adult life stages of certain fish species using traditional fish bioassays because of their size (Dave 1993). ELS fish are much smaller, can equilibrate to external experimental conditions more quickly, and generally have lower dissolved oxygen requirements than older conspecifics (Braunbeck et al. 2005). In addition, embryos and eleutheroembryos do not have exogenous dietary considerations, as experiments on older life stage fish would require. This allows for the relative dietary condition of fishes used in experiments to be standardized, as they are all feeding on their yolk-sacs and not exogenously (Belanger et al. 2010). Using ELS fish bioassays may also aid in examining the effects of HABs on fish growth, development and population recruitment (Lefebvre et al. 2004, Berry et al. 2007). As >95% of fish species fertilize embryos externally, researchers could assess the effects of HABs on a variety of marine fish including those that are known to be ecologically or economically important.

In this study, a few preliminary experiments exhibited poor embryo survival in controls. This was likely due to unforeseen interactions (i.e. the stimulation of bacterial or mycotic growth in control culture media) rather than infirm organisms, as survival was acceptable in other respective treatments. Bacterial growth in culture media of *C. polykrikoides* has been demonstrated before (Tang & Gobler 2012) and although embryos were rinsed in sterile culture media prior to experiments during the present study, it is likely that they still contained microbial contaminants. The application of increased antimicrobial solution every three days to replicates was found to greatly improve

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survival of *M. beryllina* embryos and eleutheroembryos. Future embryo experiments using nutrient ameliorated culture media should consider using similar antimicrobial applications if control survival of embryos is unexpectedly poor.

4.6 Chapter 4 Figures
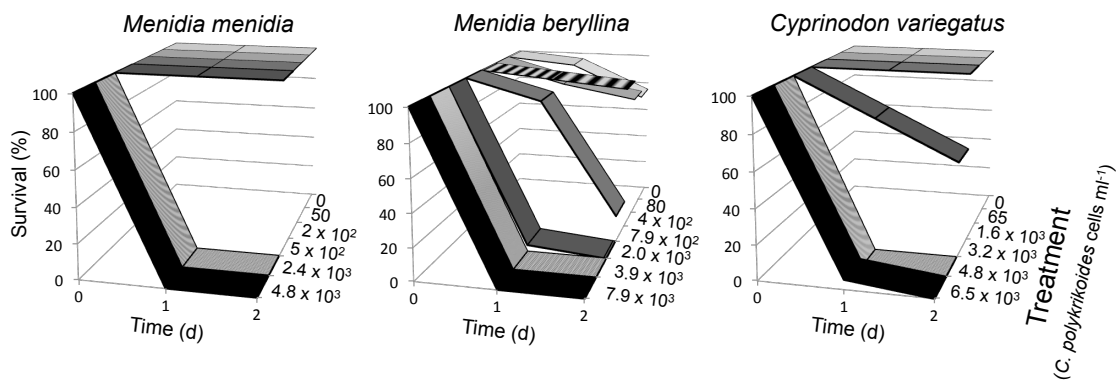
Figure 4. Survival of *Menidia menidia*, *Menidia beryllina* and *Cyprinodon variegatus* eleutheroembryos in static *Cochlodinium polykrikoides* acute toxicity experiments.
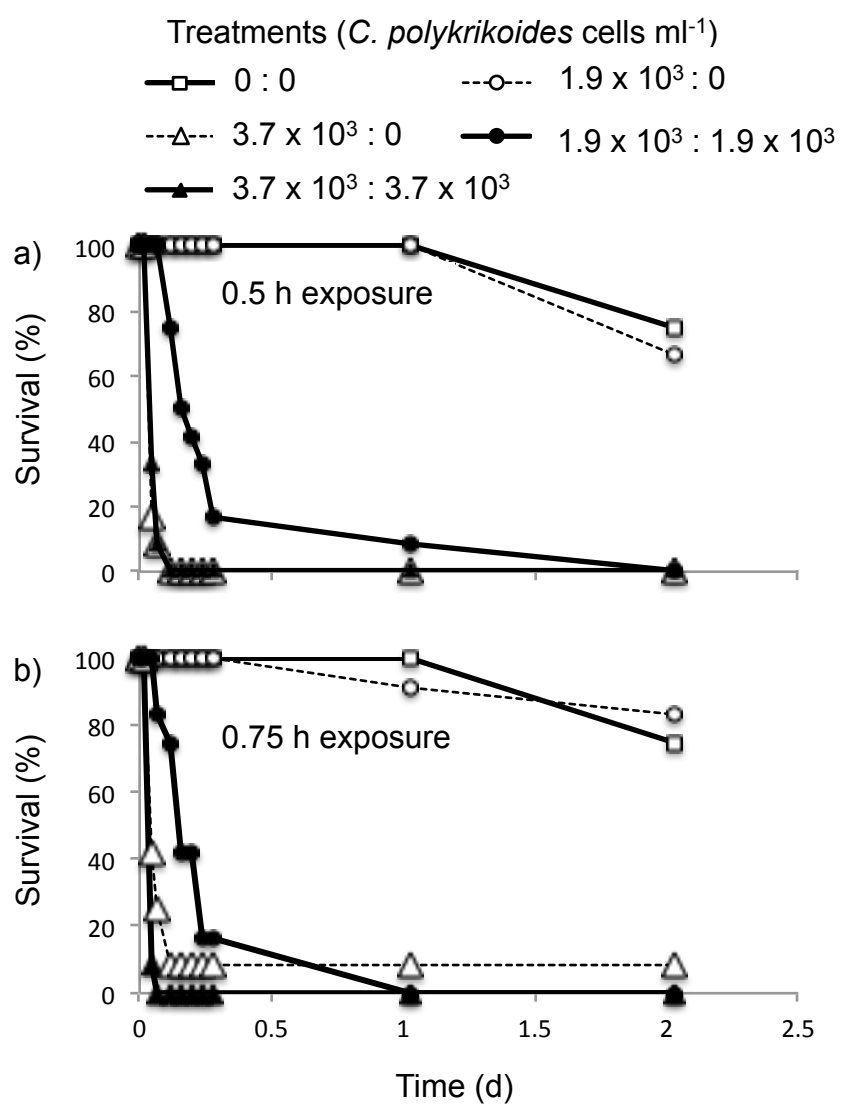
Figure 4.2 Survival of *Menidia menidia* eleutheroembryos after a) 0.5 h and b) 0.75 h exposures to *Cochlodinium polykrikoides* culture treatments. Treatments indicate the *C. polykrikoides* cell densities before and after (before : after) eleutheroembryos were transferred following the designated exposure time.
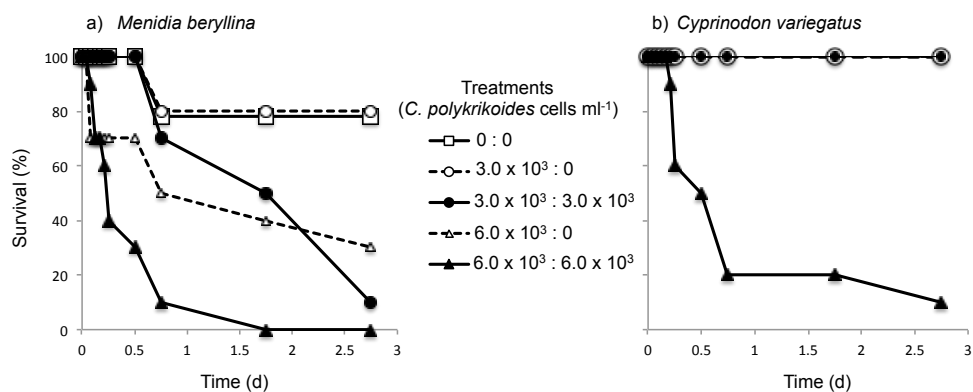
Figure 4.3 Survival of a) *Menidia beryllina* and b) *Cyprinodon variegatus* eleutheroembryos after a 0.25 h exposure to *Cochlodinium polykrikoides* culture. Treatments indicate the *C. polykrikoides* cell densities before and after (before : after) eleutheroembryos were transferred at 0.25 h.
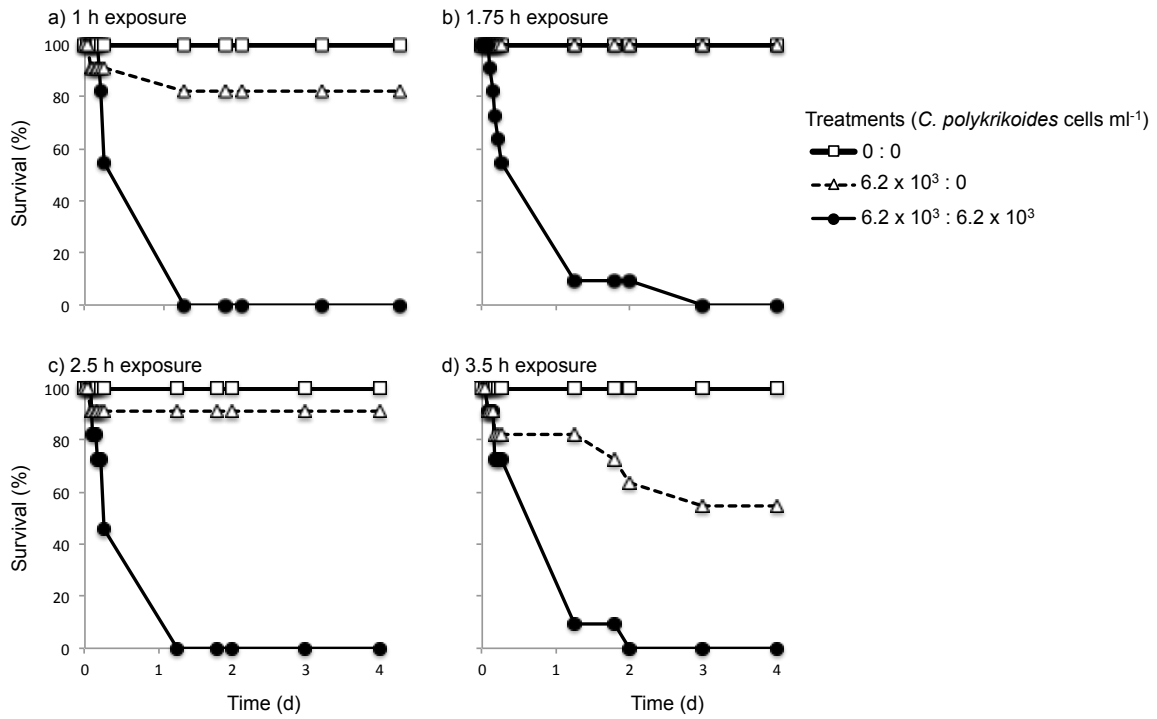
Figure 4.4 Survival of *Cyprinodon variegatus* eleutheroembryos after a) 1 h, b) 1.75 h, c) 2.5 h, and d) 3.5 h exposures to *Cochlodinium polykrikoides*. Treatments indicate the *C. polykrikoides* cell densities before and after (before : after) eleutheroembryos were transferred following the designated exposure times.
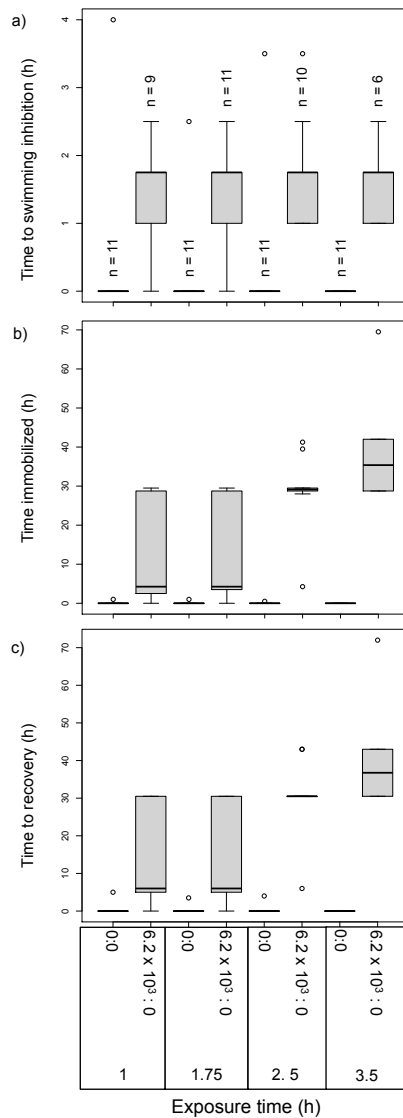
Figure 4.5 Sublethal effects of *Cochlodinium polykrikoides* culture to a) time to swimming inhibition, b) total time immobilized and c) time to swimming recovery for surviving *Cyprinodon variegatus* eleutheroembryos. Lines inside box plots represent the median values, while the upper and lower segments represent the 0.75 and 0.25 quartiles respectively. Treatments indicate the *C. polykrikoides* cell densities before and after (before : after) eleutheroembryos were transferred following the designated exposure times. Open circles represent data outliers identified by the R statistical software.

4.7 Chapter 4 Tables

Table 4.1 Inventory of *Cochlodinium polykrikoides* toxicity experiments with early life stages of *Menidia menidia* (MM), *M. beryllina* (MB) and *Cyprinodon variegatus* (CV) species.

Experiment #	Species	Max. *C. polykrikoides* (cells ml^{-1})	Treatments (% of max. *C. polykrikoides*)	Fish per treatment (n)	Fish used (n)	Sampling frequency (d)	Duration (d)
Embryo toxicity experiments							
1	MM	3×10^3	(0,1,5,10,25,50,100)	18,21,20,20,19,22,18	138	0,1,7,8,10	10
2	MB	5×10^3	(0,1,5,10,25,50,100)	21,22,22,22,22,22,23	154	0,2,4,7,8,9	9
3	CV	6×10^3	(0,1,25,50,75,100)	15,13,13,9,9,13	72	0,2,3,4,5,6,7,8	8
Eleutheroembryo acute toxicity experiments							
4	MM	5×10^3	(0,1,5,10,50,100)	24,24,24,24,24,24	144	0,1,2	2
5	MB	8×10^3	(0,1,5,10,25,50,100)	24,24,24,24,24,24,24	168	0,1,2	2
6	CV	6×10^3	(0,1,25,50,75,100)	18,18,18,18,18,18	108	0,1,2	2
Eleutheroembryo exposure/recovery experiments							
7	MM	4×10^3	0.5h(0:0), 0.5h(50:0), 0.5h(50:50), 0.5h(100:0), 0.5h(100:100), 0.75h(0:0), 0.75h(50:0), 0.75h(50:50), 0.75h(100:0), 0.75h(100:100)	12,12,12, 12,12, 12,12,12, 12,12	120	0,0.02,0.04,0.07,0.11, 0.16,0.2,0.24,0.28,1.03,2.03	2.03
8	MB	6×10^3	0.25h(0:0), 0.25h(50:0),0.25h(50:50), 0.25h(100:0),0.25h(100:100)	10,10,10, 10,10	50	0,0.04,0.08,0.13,0.17, 0.21,0.25,0.5,0.75,1.75,2.75	2.75
	CV	6×10^3	0.25h(0:0), 0.25h(50:0),0.25h(50:50), 0.25h(100:0),0.25h(100:100)	10,10,10, 10,10	50		
9	CV	6×10^3	1h(0:0), 1h(100:0),1h(100:100), 1.75h(0:0), 1.75h(100:0), 1.75h(100:100), 2.5h(0:0), 2.5h(100:0), 2.5h(100:100), 3.5h(0:0), 3.5h(100:0), 3.5h(100:100)	11,11,11, 11,11,11, 11,11,11, 11,11,11, 11,11,11	132	0,0.07,0.1,0.15,0.17,0.21,0. 25,1.25,1.79,2.0,3.0,4.0	4

Table 4.2 Summary of survival analyses in *Cochlodinium polykrikoides* toxicity experiments (Experiments 1-6) with *Menidia menidia* (MM), *M. beryllina* (MB) and *Cyprinodon variegatus* (CV) early life stage fish. Chi-square (χ^2), degrees of freedom (*df*), statistical significance (p value) and number of fish in each analysis (N) are given. Values that were not significant (ns) had a p value > 0.05 and "-" indicates values that could not be calculated.

Experiment #	Species	Test	χ^2	*df*	p value	N
Embryo toxicity experiments						
1	MM	Time to death (embryo)	-13890	1	ns	138
		Time to hatch	15.87	1	< 0.0001	133
		Time to death (eleutheroembryo)	89.67	1	0	133
2	MB	Time to death (embryo)	-6351	1	ns	154
		Time to hatch	11.58	1	0.0007	116
		Time to death (eleutheroembryo)	57.9	1	< 0.0001	116
3	CV	Time to death (embryo)	0.98	1	ns	72
		Time to hatch	0.02	1	ns	48
		[a]Time to death (eleutheroembryo)	-	-	-	48
Eleutheroembryo acute toxicity experiments						
4	MM	Time to death (eleutheroembryo)	184.25	1	0	144
5	MB	Time to death (eleutheroembryo)	131.23	1	0	144
6	CV	Time to death (eleutheroembryo)	131.46	1	0	108
a = Insufficient number of days post-hatch to conduct statistical test						

Table 4.3 Statistical significance of time to eleutheroembryo death in exposure/recovery experiments using pairwise t-tests with Bonferroni adjusted error rates for *Menidia menidia* (MM), *Menidia beryllina* (MB) and *Cyprinodon variegatus* (CV) species. Full (i.e. 50:50 and 100:100) and partial (i.e. 50:0 and 100:0) exposure treatments were compared to their respective control (0:0) treatment. 0, 50 and 100 represent the percentage of the maximum *C. polykrikoides* cell density used for each respective experiment, found in Table 4.1.

Experiment #	Species	Test	Exposure time (hr)	50:0 χ^2	*df*	p value	50:50 χ^2	*df*	p value	100:0 χ^2	*df*	p value	100:100 χ^2	*df*	p value
Eleutheroembryo exposure/recovery experiments															
7	MM	Time to death (eleutheroembryo)	0.5	-0.86	1	ns	26.7	1	<0.0001	71.2	1	<0.0001	73.2	1	<0.0001
			0.75	0.12	1	ns	32.1	1	<0.0001	25	1	<0.0001	93.3	1	<0.0001
8	MB	Time to death (eleutheroembryo)	0.25	0.32	1	ns	3.72	1	ns	2.95	1	ns	16	1	0.005
	CV		0.25	-	-	ns	-	-	ns	-	-	ns	23.3	1	<0.0001
9	CV	Time to death (eleutheroembryo)	1	na	na	na	na	na	na	3.01	1	ns	38.6	1	<0.0001
			1.75	na	na	na	na	na	na	-	-	ns	32.8	1	<0.0001
			2.5	na	na	na	na	na	na	1.45	1	ns	36.9	1	<0.0001
			3.5	na	na	na	na	na	na	8.42	1	0.04	34.3	1	<0.0001

Table 4.4 Statistical significance of sublethal effects of *Cochlodinium polykrikoides* to *Cyprinodon variegatus* eleutheroembryos across all exposure types (i.e. 0:0, 100:0 and 100:100) and exposure times (i.e. 1 h, 1,75 h, 2.5 h and 3.5 h) using pairwise t-tests with Bonferroni adjusted error rates. ns denotes p values that were not significant ($p > 0.05$) and na indicates that comparisons were not applicable because of dead individuals. Exposure type values (i.e. 0 and 100) refer to the percentage of the maximum *C. polykrikoides* cell density used for experiment 9 (Table 4.1).

			Exposure time (h)											
			1			1.75			2.5			3.5		
Time to swimming inhibition			0:0	100:0	100:100	0:0	100:0	100:100	0:0	100:0	100:100	0:0	100:0	100:100
Exposure time (h)	1	0:0												
		100:0	0.0474											
		100:100	na	na										
	1.75	0:0	ns	0.0145	na									
		100:0	ns	ns	na	0.0197								
		100:100	na	na	na	na	na							
	2.5	0:0	ns	0.0322	na	ns	0.0451	na						
		100:0	0.0047	ns)	na	0.0451	ns	na	0.003					
		100:100	na	na	na	na	na	na	na	na				
	3.5	0:0	ns	0.0017	na	ns	0.0021	na	ns	0.0001	na			
		100:0	ns	ns	na	0.0329	ns	na	ns	ns	na	0.0053		
		100:100	na	na	na	na	na	na	na	na	na	na	na	
Time immobilized			0:0	100:0	100:100	0:0	100:0	100:100	0:0	100:0	100:100	0:0	100:0	100:100
Exposure time (h)	1	0:0												
		100:0	ns											
		100:100	na	na										
	1.75	0:0	ns	ns	na									
		100:0	0.0043	ns	na	0.0043								
		100:100	na	na	na	na	na							
	2.5	0:0	ns	ns	na	ns	0.0041	na						
		100:0	<0.0001	0.0013	na	<0.0001	0.0109	na	<0.0001					
		100:100	na	na	na	na	na	na	na	na				
	3.5	0:0	na	ns	na	ns	0.0039	na	ns	<0.0001	na			
		100:0	<0.0001	<0.0001	na	<0.0001	<0.0001	na	<0.0001	ns	na	<0.0001		
		100:100	na	na	na	na	na	na	na	na	na	na	na	
Time to recovery			0:0	100:0	100:100	0:0	100:0	100:100	0:0	100:0	100:100	0:0	100:0	100:100
Exposure time (h)	1	0:0												
		100:0	ns											
		100:100	na	na										
	1.75	0:0	ns	0.0475	na									
		100:0	0.002	ns	na	0.0017								
		100:100	na	na	na	na	na							
	2.5	0:0	ns	0.0492	na	ns	0.0018	na						
		100:0	<0.0001	0.0014	na	<0.0001	0.0103	na	<0.0001					
		100:100	na	na	na	na	na	na	na	na				
	3.5	0:0	ns	0.037	na	ns	0.0013	na	ns	<0.0001	na			
		100:0	<0.0001	<0.0001	na	<0.0001	<0.0001	na	<0.0001	ns	na	<0.0001		
		100:100	na	na	na	na	na	na	na	na	na	na	na	

Chapter 5. First assessment of behavioral toxicity from sublethal exposures to harmful dinoflagellate, *Cochlodinium polykrikoides*, on swimming behavior of three estuarine forage fish species

5.1 Introduction

To understand the effects of contaminants on fish species and determine acceptable exposure concentrations in the field, scientists utilize an array of toxicity experiments and approaches (Sprague 1990, EPA 2002). While traditional toxicity experiments are valuable for obtaining baseline toxicology data, they are often difficult to interpret in an ecological context (Kimball & Levin 1985, de Vlaming & Norberg-King 1999). In this regard, behavioral experiments are a valuable auxiliary approach to traditional toxicity research, providing ecologically relevant endpoints and novel toxicity information (Little et al. 1990, Weis & Weis 1995b, Kane et al. 2005). Fish are ideal model organisms for behavioral toxicity experiments, as they are relatively easy to culture and are of high ecological relevance (Scott & Sloman 2004, Kane et al. 2005). In addition, because of their sophisticated olfactory systems (Noakes & Godin 1988, Tierney et al. 2010), fish are often seen as ideal for assessing sublethal toxicity, as scientists can effectively evaluate whether or not fish can detect or respond to toxicant exposures (Noakes & Baylis 1990, Kane et al. 2005).

The impacts of anthropogenic contaminants on fish behavior have been explored for several decades (Rand 1985, Atchison et al. 1987, Little & Finger 1990, Webber & Haines 2003, Sloman & Wilson 2006). Many of these studies have demonstrated serious impairment of sensory abilities in fish following sublethal exposures to contaminants, ultimately leading to the compromised survival of exposed individuals (McPherson et al. 2004, Leduc et al. 2006, Leduc et al. 2009, Tierney et al. 2010, Tierney et al. 2011). Surprisingly, only a few studies have evaluated the effects of harmful algal blooms (HABs), or their toxins, on fish behavior (Lefebvre et al. 2001, Lefebvre et al. 2004, Salierno 2005, Samson et al. 2008, Lefebvre et al. 2012). These studies have found a variety of behavioral responses following sublethal exposures to HAB

species, ranging from impaired swimming to reduced feeding ability. Unfortunately, only data from traditional toxicity assessments exist for the vast majority of HAB species plaguing coastal waters (Landsberg 2002).

In many regions of world, blooms of the ichthyotoxic dinoflagellate, *Cochlodinium polykrikoides*, are now annual events, presenting a significant threat to coastal marine organisms (Lee et al. 2002, Gobler et al. 2008, Tomas & Smayda 2008, Richlen et al. 2010, Kudela & Gobler 2012). Blooms caused by *C. polykrikoides* can form dense heterogeneous patches in coastal ecosystems (Gobler et al. 2008, Mulholland et al. 2009, Tang & Gobler 2010). These ichthyotoxic bloom patches can vary in size (i.e. from m^2 to km^2 scales) and duration (i.e. weeks to several months), creating dynamic exposures to fish and other marine organisms (Gobler et al. 2008, Richlen et al. 2010, Koch 2012). While the ichthyotoxicity of *C. polykrikoides* to a variety of fish species and life-stages is now well established (Onoue et al. 1985, Gobler et al. 2008, Tang & Gobler 2009, Rountos et al. in press), the toxinology is not yet confirmed (Tang & Gobler 2009, Kim & Oda 2010). However, several studies have demonstrated that the toxicants are extracellular, biologically active, and produced by physiologically active *C. polykrikoides* cells (Kim et al. 2002, Tang & Gobler 2009, 2010).

Our understanding of the toxicity of *C. polykrikoides* to fish is based entirely on static toxicity experiments or observations of fish kill events (Onoue et al. 1985, Kim et al. 1999, Whyte et al. 2001, Landsberg 2002, Gobler et al. 2008, Tang & Gobler 2009, Richlen et al. 2010, Rountos et al. in press). Although laboratory studies clearly demonstrate the ichthyotoxicity of this HAB species, they often fail to address the dynamic nature of exposures in the field, or the potential for fish to avoid or escape these blooms. To my knowledge, only one laboratory study, Rountos et al. (in press), has examined the toxicity of *C. polykrikoides* to fish following ecologically relevant exposure times (i.e. minutes to hours). These authors found that short exposures to *C. polykrikoides* were able to cause loss of swimming ability and even significant mortality to eleutheroembryos of three fish species. The loss of swimming ability is the first documented evidence of sublethal behavioral effects of *C. polykrikoides* to fish (Rountos et al. in press). It is clear that the potential threats that *C. polykrikoides* blooms pose to fish behavior remains significantly unexplored, potentially complicating our ability to sustainably manage resources in these ecosystems (Burkholder 1998, Kudela & Gobler 2012).

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In this study, the behavioral effects of sublethal exposures of *C. polykrikoides* to larvae of three species of forage fish common to U.S. East Coast estuaries were assessed. Using a video-based movement analysis system, changes in fish behavior (i.e. fish speed (cm s^{-1}), acceleration (cm s^{-2}), the total time fish were active (s), and the total distance fish swam (cm) resulting from exposure to *C. polykrikoides* were assessed. This research provides the first assessment of the behavioral effects of *C. polykrikoides* on larval fish, and establishes and validates a framework with fish models for future behavioral toxicity studies with *C. polykrikoides*.

5.2 Materials and Methods
5.2.1 Dinoflagellate cultures

Clonal cultures grown in laboratories were used in this study to isolate the direct effects of *Cochlodinium polykrikoides* from the potentially confounding effects of a complex plankton community found in natural bloom water. The dinoflagellate *C. polykrikoides* (strain CP1) was isolated from bloom water collected in Flanders Bay, Peconic Estuary, NY, USA in 2006 (Tang & Gobler 2009), while the dinoflagellate *Gymnodinium aureolum*, which served as a non-toxic dinoflagellate control (Tang & Gobler 2009), was isolated in the Elizabeth River tributary, Chesapeake Bay, VA, USA in 2006 (Tang et al. 2008). Clonal cultures of *C. polykrikoides* and *G. aureolum* were maintained in sterile GSe culture medium prepared according to Tang & Gobler (2009). Briefly, the culture medium was prepared with autoclaved and filtered (0.22 μm) coastal Atlantic Ocean seawater (Salinity: 30) supplemented with stock nutrients and an antibiotics solution (a mixture of 10,000 I.U. penicillin and 10,000 μg ml^{-1} streptomycin, Mediatech. Inc., Hemdon, VA, USA) with a final concentration of 2% (Tang & Gobler 2009). Cultures of *C. polykrikoides* and *G. aureolum* were incubated at 21°C following a 12 h light: 12 h dark photoperiod with a light intensity ~100 μmol quanta m^{-2} s^{-1} (Tang & Gobler 2009). Cell densities in *C. polykrikoides* and *G. aureolum* clonal cultures of were quantified by first fixing a 10 ml aliquot of clonal culture with Lugol's solution and then counting all dinoflagellate cells from three 0.25 ml subsamples on a Sedgewick-Rafter counting chamber. Denser dinoflagellate cultures were diluted with fresh GSe so that similar concentrations could be achieved for experiments (Table 5.1).

5.2.2 Fish maintenance and care

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All fish culturing, handling, experimental design, and final disposal in these experiments followed procedures approved by the Institutional Animal Care and Use Committee at Stony Brook University (Stony Brook, NY, USA) using organisms approved for toxicity research (EPA 2002). Fish used in experiments were approximately two months old and were maintained in the Stony Brook Southampton wet lab facility (Southampton, NY, USA) at least two weeks prior to any experiment. Atlantic silversides (*Menidia menidia*) were obtained from hatching embryos originally collected by strip spawning adult fish collected in May 2013 by beach seine from Shinnecock Bay, NY, USA. Strip spawning procedures followed the methods described in Costello et al. (1957). Inland silversides (*Menidia beryllina*) were purchased from hatchery stocks maintained by Aquatic Resource Organisms (Hampton, NH, USA), while sheepshead minnow (*Cyprinodon variegatus*) were obtained from Aquatic Bio Systems (Fort Collins, CO, USA).

Newly hatched Atlantic silversides were cultured in modified 19 l buckets with three lateral holes covered with fine mesh screens to allow for water exchange in seawater tables. Unfiltered seawater from Shinnecock Bay supplied these buckets. Particulate material at the bottom of the buckets was syphoned daily to maintain water quality and fish were fed pulverized fish flakes ad libatum. After a month, Atlantic silversides were transferred to larger culturing tanks and fed commercial fish flakes. Two month old fish larvae were raised with conspecifics (~200 individuals per aquarium) in separate aerated glass aquaria (38 l, 33 x 19 x 11.5 cm) equipped with a filter and one automatic feeder (Petco® Auto Fish Feeder, Petco, San Diego, CA, USA) containing Tetramin® flake food (Tetra, Melle, Germany) each. Fish were monitored daily and were automatically fed flakes everyday at regular intervals during daylight hours (i.e. at 07:00, 10:00, 13:00, and 16:00). Water quality was maintained by replacing 50% of the water in each aquarium with clean unfiltered Shinnecock Bay water (~20 l) each week. Laboratory temperatures were maintained at 20-25°C with an approximate photoperiod of 12 h light: 12 h dark. Mortality of fish was very low (<5%) during culturing and there were no signs of stress or disease in fish cultured in aquaria.

5.2.3 Design of video system

Three freestanding video stages were created to serve as platforms for experiments. Each stage was equipped with a single HD video camcorder (Sony® Handycam, Model HDR-CX210,

HDR-CX220 or HDR-CX230) mounted above it (Figure 5.1). Video stages were created by first lining up and then affixing two white polyethylene cylinders to both sides of a piece of clear acrylic sheet (41 x 41 x 0.6 cm) using adhesive caulk (Figure 5.2). Cylinders were obtained from white buckets with 19 l capacity that were cut to the lengths listed in Figure 5.2. Once the caulk dried, several sheets of white copy paper were taped to the bottom side of the acrylic stage, creating a white platform inside the cylinder walls. The top cylinder isolated fish in arenas from peripheral visual disturbances or human motion in the room. Although experiments were conducted in a lit laboratory during daytime hours, stages were also illuminated from the bottom to increase video contrast and eliminate shadows (Skjaeraasen et al. 2008, Herbert et al. 2011). One light bulb (Ecosmart™ CFL spiral, 19W (100W equivalent), 120V) housed in a work light basket guard was placed on the ground and in the center of the lower white cylinder for each video stage (Figure 5.2).

5.2.4 Experimental design

To assess the effects of *C. polykrikoides* on the behavior of larval forage fish, three behavioral experiments were conducted, each using different species of forage fish common to the U.S. East Coast. All behavioral experiments were conducted in ~20°C water at the Stony Brook Southampton Marine Station (Southampton, NY, USA) during daylight hours with only one person in the room. Atlantic silversides, inland silversides, and sheepshead minnow used for experiments stopped receiving food approximately 12 h before the first trial of their respective experiments, to ensure that their stomachs were empty. As only three video cameras and stages could operate at one time, treatments were randomized across trials throughout an experiment to prevent temporal bias. Dissolved oxygen was measured in the flasks which contained the different treatment stocks (i.e. GSe, *C. polykrikoides* clonal culture, etc.) prior to experiments using a self-stirring BOD probe connected to a YSI Model 5100 benchtop dissolved oxygen meter (YSI Inc, OH, USA).

Experiments were designed so that fish served as their own behavioral controls, greatly increasing the statistical power by reducing inter-individual variability (Kane et al. 2005). To do this, two assessments of fish behavior were made in every trial for every treatment, one to establish a baseline of fish behavior (i.e. baseline portion) in GSe control conditions and a behavioral assessment following exposure to the respective experimental treatment (i.e.

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experimental portion). To account for behavioral differences resulting from inter-individual variability, the change in values of behavioral variables was analyzed between the experimental portions and the control portions. All experiments followed the same general steps outlined in Figure 5.3. Before every trial, three fish were selected using a soft dip net and gently placed in a clear arena (i.e. the bottom half of a polystyrene petridish, total volume = 150 ml, diameter = 14 cm, height = 1.6 cm, Figure 5.2b) containing 75 ml of GSe. Fish were in contact with the net surface for only a few seconds, to minimize stress (Tierney 2011). Three fish were used in each arena for each trial, as forage fish species are known to exhibit different behaviors or stress when not in schools (Reinfelder & Fisher 1994, Billerbeck et al. 2001, Kane et al. 2005). Fish were recorded dorsoventrally in this arena from a mounted camera above. This arena encouraged lateral movement and discouraged vertical movement of fish, as the behavioral analysis software only tracks fish in two dimensions. One fish arena was placed in the center of each video stage platform. Fish acclimated in arenas for 30 minutes and no mortality or irregular behaviors, such as disorientation, impairment, etc., were observed during that time in any experiment. Fish were previously found to be able to survive in arenas with 75 ml of GSe for at least 96 hours (length of experiment; unpublished data). After acclimation, video recording of the baseline portion of the trial was initiated and 75 ml of GSe was added to each arena using a pipette bulb and 50 ml pipette. Fish in arenas were recorded without further disturbance for 20 minutes. Once the baseline portion was finished, 75 ml of GSe (50% of total volume) was removed from each arena and replaced by 75 ml of treatment. Treatments used for the experimental portion of trials varied by experiments (Table 5.1), but all experiments included at least a GSe control and *Cochlodinium polykrikoides* treatment. A completed trial produced a video 40 minutes in length (i.e. baseline portion = 20 minutes and experimental portion = 20 minutes). Once a trial was complete, the fish arenas were moved to a lab table where they were left undisturbed (i.e. no aeration and food) for 24 hours to assess survival between treatments. Fish survival was assessed and the total length (nearest 0.1 cm) and mass (wet weight to nearest 0.01 g) of each fish was recorded.

Details for each experiment can be found in Table 5.1. Behavioral experiments varied in the species used, number of treatments, and the number of trials. Only two treatments were used in the Atlantic silverside experiment, a GSe control and a *C. polykrikoides* clonal culture treatment. A non-toxic dinoflagellate control treatment (*G. aureolum*) was subsequently used in

the inland silverside and sheepshead minnow experiments in addition to the GSe control and *C. polykrikoides* clonal culture treatments. The *G. aureolum* treatments served as a dinoflagellate control for experiments, as it is non-toxic, but similar in size and shape to *C. polykrikoides* (Tang et al. 2008, Tang & Gobler 2009). Additionally, a filtered seawater (FSW) control treatment was used in the inland silverside experiment in order to ensure that fish behavior in the GSe control was not different from normal fish behavior exhibited in FSW.

5.2.5 Video processing and analysis

Video files (.mpg, frame rate = 30 frames s^{-1}) were converted to AVI format (.avi) required for analysis with LoliTrack v.4 software (Loligo®Systems, Denmark). Videos were converted to AVI (size = 1280x720, codec = xvid, bitrate = 12000, frame rate = 30 frames s^{-1}) using video conversion freeware (Any Video Converter v. 5.0.6, Anvsoft Inc.). All videos were first edited into two distinct video segments, the baseline portion and the experimental portion, each approximately 20 minutes long. To prevent analysis of fish behavior that was stimulated immediately before or after pipetting, video segments were then edited down to ~10 minutes by removing the first and last 5 minutes in each video.

Before fish in video segments were tracked in LoliTrack v.4 software, videos were loaded in the software and pixel distances were calibrated using the diameter of the fish arena (i.e. 14 cm) as a standard across all videos. This ensured that distances calculated in videos were comparable. The same general optional settings for masking, dilations, filtering, RBG scales etc. were used to track fish in all videos from each experiment, based on the fewest amount of tracking errors.

LoliTrack v.4 software quantified a summary of behavioral data for a variety of variables for each individual fish in the video, including mean speed (cm s^{-1}), mean acceleration (cm s^{-2}), total time active (s) and total distance swam (cm). These variables were selected, as they are appropriate measures of general fish behavioral characteristics and have been used in previous behavioral experiments (Skjaeraasen et al. 2008, Herbert et al. 2011, Poulsen et al. 2011). In addition, including other variables (i.e. fish orientation, turning frequency etc.) substantially increases the time needed for the software to analyze tracked videos. Fish were identified by the software as being "active" as long as their movement in one video frame exceeded a threshold

distance of 1 pixel in any direction. In total, video processing, tracking, and analysis for each experiment required approximately 1-2 months of continuous operation of Lolitrack v.4 software on a laptop computer (Lenovo T410, 8GB RAM, Intel®Core™i5 processor, M520@2.40GHz, Windows 7 operating system), depending on the number of video segments.

5.2.6 Data analysis and statistical approach

Values for mean speed, mean acceleration, total time active, and total distance swam by each of the three fish in each video were averaged to obtain a mean value for each behavioral variable in each video segment. Results were presented as the change in the mean values of behavioral variables between the baseline and experimental portions of a trial, and trials served as the replicates (Table 5.1). Analyzing the changes in mean values of behavioral variables allowed for statistical comparisons to be made between treatments, while also controlling for inter-individual variability in fish behavior. Homogeneity of variances was assessed using Bartlett's test (Bartlett 1937) and when homogeneity of variances were violated, a Welch One-way ANOVA (Welch 1951) was used to assess if changes in mean fish behavioral variables were statistically different between experimental treatments. If significant differences were found ($p < 0.05$), a Dunnett's T3 (Dunnett 1980) pairwise multiple comparison test adjusted for unequal variances was used. All statistical analyses were conducted using the R statistical software (CRAN R, version 2.15.0, www.R-project.org/) with a Dunnet's T3 package (Lau 2013).

5.3 Results
5.3.1 Atlantic silverside (*Menidia menidia*) experiment

Changes in the mean speed (Figure 5.4a, Welch One-way ANOVA, $F = 17.46$, $p < 0.0005$), the mean total time active (Figure 5.4c, Welch One-way ANOVA, $F = 13.71$, $p < 0.001$), and the mean total distance swam (Figure 5.4d, (Welch One-way ANOVA, $F = 13.84$, $p < 0.002$) of fish exposed to *C. polykrikoides* were significantly greater compared to fish exposed to the GSe control. No significant difference was found in changes in mean acceleration of fish between these treatments (Figure 5.3b, One-way ANOVA, $F = 3.54$, $p = 0.07$). Survival of fish at 24 h was 91% (41 out of 45) for the GSe control and 44% (20 out of 45) for the *C. polykrikoides* treatment (8.5×10^2 cells ml^{-1} $\pm 1.1 \times 10^2$ SD). Atlantic silversides used in this experiment were 1.91 cm ± 0.25 SD and 0.03 g ± 0.02 SD. No significant differences were found

between the total length (One-way ANOVA, $F = 0.31$, p = 0.58) and mass (One-way ANOVA, F = 1.12, p = 0.29) of fish used between treatments. Dissolved oxygen in the GSe control and *C. polykrikoides* treatment flasks measured before the first trial were comparable at 8.83 and 8.33 mg l^{-1} respectively.

5.3.2 Inland silverside (*Menidia beryllina*) experiment

Significant differences were found in changes in mean speed of fish between treatments (Figure 5.5a, Welch One-way ANOVA, $F = 5.3$, p < 0.005), the mean total time fish were active (Figure 5.5c, Welch One-way ANOVA, $F = 12.59$, p < 0.0001), and the mean total swimming distance (Figure 5.4d, Welch One-way ANOVA, $F = 10.12$, p = 0.0001), but not changes in mean acceleration of fish (Figure 5.4b, Welch One-way ANOVA, $F = 0.8$, p = 0.51). Inland silversides exposed to *C. polykrikoides* (12 x 10^2 cells ml^{-1}±3.4 x 10^2 SD) had significantly greater changes in mean speed (median = 0.52 cm s^{-1}, 95% CI = 0.15 to 1.32) compared to fish in the GSe control (median = -0.27 cm s^{-1}, 95% CI = -0.47 to 0.1, Dunnett's T3 pairwise multiple comparisons, p < 0.05) and FSW control (median = -0.46 cm s^{-1}, 95% CI = -0.62 to -0.05, Dunnett's T3 pairwise multiple comparisons, p < 0.05), but not the *G. aureolum* control (median = 0.54 cm s^{-1}, 95% CI = 0.01 to 1.16, Dunnett's T3 pairwise multiple comparisons, p > 0.05) (Figure 5.5a). No significant differences in changes in mean speed of fish were found between the *G. aureolum* treatment and any other treatment (Dunnett's T3 pairwise multiple comparisons, p > 0.05). Similarly, changes in the mean speed of fish in both GSe and FSW controls were not significantly different from each other (Dunnett's T3 pairwise multiple comparisons, p > 0.05).

Fish were significantly more active in *C. polykrikoides* (median =107.79 s, 95% CI = 47.98 to 166.34) and *G. aureolum* (median = 73.11 s, 95% CI = -4.81 to 110.58) treatments compared to the FSW (median = -36.87 s, 95% CI = -59.88 to -23.43) control (Dunnett's T3 pairwise multiple comparisons, p < 0.05). Fish were significantly less active in the GSe treatment (median = -17.66 s, 95% CI = -45.12 to -6.77) compared to the *C. polykrikoides* treatment (Dunnett's T3 pairwise multiple comparisons, p < 0.05), but not the *G. aureolum* treatment. No statistically significant differences were found between the *C. polykrikoides* and *G. aureolum* treatments or between GSe and FSW controls (Dunnett's T3 pairwise multiple comparisons, p > 0.05). Similarly, fish in *C. polykrikoides* treatments swam significantly greater distances (median = 878.35 cm, 95% CI = 350.14 to 1540.14) than fish in GSe and FSW controls

(Dunnett's T3 pairwise multiple comparisons, $p < 0.05$), but not the *G. aureolum* treatment (Dunnett's T3 pairwise multiple comparisons, $p > 0.05$). No significant differences were found in the mean swimming distance of fish between the GSe (median = -115.62, 95% CI = -367.71 to -48.91) and FSW (median = -329.31, 95% CI = -459.11 to -162.45, Dunnett's T3 pairwise multiple comparisons, $p > 0.05$) treatments. Changes in the mean swimming distance of fish in the *G. aureolum* treatment were significantly greater than the FSW control (Dunnett's T3 pairwise multiple comparisons, $p < 0.05$), but not the GSe control (Dunnett's T3 pairwise multiple comparisons, $p > 0.05$).

Survival of fish at 24 h was >96% for all treatments. Inland silversides used in this experiment were 2.09 cm ±0.31 SD and 0.05 g ±0.02 SD. No significant differences were found between the total length (One-way ANOVA, $F = 1.75$, $p = 0.16$) and mass (One-way ANOVA, $F = 1.36$, $p = 0.26$) of fish used between treatments. Dissolved oxygen in the GSe control, FSW control, *C. polykrikoides* treatment and *G. aureolum* treatment flasks were all comparable at 8.82, 8.75, 8.93 and 9.08 mg l^{-1} respectively. In addition, cell densities of *C. polykrikoides* (12 x 10^2 cells ml^{-1} ±3.4 x 10^2 SD) and *G. aureolum* (13 x 10^2 cells ml^{-1}±0.96 x 10^2 SD) were comparable.

5.3.2 Sheepshead minnow (*Cyprinodon variegatus*) experiment

No significant differences ($p > 0.05$) were found between GSe control, *C. polykrikoides* (5.3 x 10^2 cells ml^{-1} ±0.95 x 10^2 SD) and *G. aureolum* (11 x 10^2 cells ml^{-1} ±1.1 x 10^2 SD) treatments in the change in mean speed of fish (Figure 5.6a), change in mean acceleration (Figure 5.6b), change in the mean total time fish were active (Figure 5.6c, Welch's One-way ANOVA, $F = 0.15$, $p = 0.87$), and the change in mean total swimming distance of fish (Figure 5.6d). Survival of fish at 24 h was 100% for all treatments. Sheepshead minnows used in this experiment were 1.97 cm ±0.28 SD and 0.1 g ±0.05 SD. No significant differences were found between the total length (One-way ANOVA, $F = 0.24$, $p = 0.74$) and mass (One-way ANOVA, $F = 0.36$, $p = 0.70$) of fish used between treatments. Dissolved oxygen in the GSe control, *C. polykrikoides* treatment, and *G. aureolum* treatment flasks were comparable at 8.44, 9.05, and 9.11 mg l^{-1} respectively. In addition, dissolved oxygen measurements, made in each arena after each trial was complete, were not significantly different from each other (Figure 5.7, One-way ANOVA, $F = 0.22$, $p = 0.81$).

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5.4 Discussion
5.4.1 Assessing the effects of *Cochlodinium polykrikoides* exposures on fish behavior

This study found no significant differences in any behavioral variables between sublethal exposures of *C. polykrikoides* to larval forage fish compared to a non-toxic dinoflagellate (*G. aureolum*) in the inland silverside and sheepshead minnow experiments. Inland silversides exposed to dinoflagellates (i.e. *C. polykrikoides* and *G. aureolum*) displayed significantly increased behavior (i.e. increased swimming speed, time active, and distance swam) to non-dinoflagellate controls, while sheepshead minnows showed behavior similar to the non-dinoflagellate controls. Survival for fish in both experiments was >96% after 24 h, suggesting that fish survival was not compromised from sublethal exposures of *C. polykrikoides*. These results indicate that the observed increases in the behavioral variables in the inland silverside experiment may be due to the presence of dinoflagellates and not necessarily their toxicity, at least at the cell densities evaluated here, since *G. aureolum* is a non-toxic dinoflagellate that is of similar size to *C. polykrikoides* (Tang et al. 2008, Tang & Gobler 2009). This result was also likely not due to any differences in oxygen between treatments, as initial oxygen concentrations in treatment flasks were comparable and well within the range suitable for fish. In addition, no significant differences in dissolved oxygen in arenas were found after trials in the sheepshead minnow experiment were completed (Figure 5.7). The observed increases in speed in the Atlantic silverside and inland silverside experiments were also likely not a result of the fish feeding on the dinoflagellates either, although this can not be discounted entirely in this study as the stomachs of fish were not examined. Although relatively little is known about the feeding habits of silverside species (i.e. *Menidia menidia* and *Menidia beryllina*), they are known to consume a variety of algae, zooplankton and detritus (Fay et al. 1983). While other planktivorous fish are known to use area-restricted or saltatory searching behaviors when feeding, in which their speed slows down as they visually search for prey items (Hunter & Thomas 1974, Browman & O'Brien 1992, Ruzicka & Gallager 2006), it is not known if silverside species utilize this type of feeding habit. Finally, although a non-toxic dinoflagellate treatment was not used in the Atlantic silverside experiment, the low survival (44%) indicated that exposure to *C. polykrikoides* was toxic to these fish in this experiment. In this case, it is possible that either the presence of *C. polykrikoides* and or their toxicity might have elicited the responses observed in this experiment.

The laboratory protocol developed here was successful in producing behavioral data that corrected for inter-individual variability in fish behavior, allowing for robust statistical analysis. The use of multiple controls, including a culture media control, filtered seawater control, and non-toxic dinoflagellate control, allowed for a more robust evaluation of behavioral results. Differences in behavior were found between inland silverside and sheepshead minnow experiments, with exposure to *C. polykrikoides* or *G. aureolum* treatments having no significant effect on changes in sheepshead minnow behavior. These results may be due to a variety of reasons, potentially including the increased resilience of sheepshead minnows to *C. polykrikoides* exposures compared to inland silversides, which has been demonstrated in a previous toxicity study using eleutheroembryos of these species (Rountos et al. in press) or the decreased *C. polykrikoides* cell density used in the sheepshead minnow experiment. In addition, the behavior of sheepshead minnow larvae may not be stimulated from exposure to dinoflagellates, as it seems to be for silverside species. Future experiments using these fish species should consider evaluating the effects on behavior following longer exposure periods and at multiple dinoflagellate cell densities to understand these differences observed.

5.4.2 The potential effects of *Cochlodinium polykrikoides* blooms to fish behavior in an ecosystem context.

Our understanding of the effects of *C. polykrikoides* blooms on fish in nature have mostly focused on quantifying dead or moribund individuals in the wild or in fish farms (Onoue et al. 1985, Whyte et al. 2001, Gobler et al. 2008, Richlen et al. 2010). This study found that silverside fish exposed to dinoflagellates had significantly altered behavior compared to non-dinoflagellate controls, suggesting a behavioral effect when these fish encounter dinoflagellate blooms. In the field, other studies have found interesting relationships between the relative abundances of living fish before and during *C. polykrikoides* bloom events (Bauman et al. 2010, Friedland et al. 2011). For instance, Friedland et al. (2011) found that catch per unit effort (CPUE) of Atlantic menhaden (*Brevoortia tyrannus*), an abundant forage fish species in the York River estuary (VA, USA), was inversely related to the concentration of *C. polykrikoides* in the water column during blooms. Atlantic menhaden CPUE was negligible during blooms compared to when blooms were absent (Friedland et al. 2011). Similarly, during an extensive (>500 km^2) bloom of *C. polykrikoides* in the Gulf of Oman, Bauman et al. (2010) found substantial declines (i.e. 72 to

86%) in fish abundance (numbers of fish 150 m^{-2}) when comparing surveys of coral reef fish before and during the *C. polykrikoides* bloom. Bauman et al. (2010) attributed these decreases in relative abundances to fish mortality primarily, based on their observation of dead fish and the large geographic extent of the bloom. They suggested that only fish on the fringes of these blooms would be successful at swimming away from exposure to blooms. This explanation however is not sufficient, as it is known that *C. polykrikoides* blooms form heterogeneous patches and can change their distribution in the water column, sometimes making large diurnal vertical migrations (~15 m)(Park et al. 2001). Therefore, it is possible that fish encountering *C. polykrikoides* blooms may have dove below these blooms in order to either avoid lethal exposure or simply avoid the presence of dinoflagellates. In addition, Bauman et al. (2010) found that two species of benthic fishes increased in the survey area during the bloom event, suggesting that exposures to benthic fish at greater depths were not similar to exposures at the surface (1 m depth), which was where bloom water samples were collected, or that these fish were more resistant or unaffected. Anecdotal evidence from fishermen also suggests that *C. polykrikoides* blooms may affect wild fish populations and their distributions. Fishermen in Rhode Island, USA reported that they no longer fished a particular cove during the summer months when *C. polykrikoides* blooms were occurring in that area, as baited traps set in that area were empty (Tomas & Smayda 2008). Similarly, pound net fishermen in Shinnecock Bay, NY, USA have reported negligible or no catches of fish when *C. polykrikoides* blooms occur in close proximity to their nets in the bay (Jon Semlear, per. com, Southampton Town Trustee, Southampton, NY). Ultimately, examining the impacts of these harmful algal blooms on fish behavior could have important implications for fisheries and their management.

Although mortalities from *C. polykrikoides* exposures to fish of all life stages generally occurs after minutes to hours in static exposures to bloom densities, short-term impacts on behavior and the possibility for avoidance behaviors are still largely unexplored. In this study, Atlantic silversides and inland silversides exposed to sublethal *C. polykrikoides* (8.5-12 x 10^2 cells ml^{-1}) and *G. aureolum* (13 x 10^2 cells ml^{-1}) densities displayed increased swimming speed, time active, and total swimming distances, compared to non-dinoflagellate controls. These behavioral responses were consistent with behaviors that would help remove an organism from an area where either stressful exposure or perceived stress was occurring, as fish are moving faster and covering greater distances. It is possible that fish exposed to sublethal concentrations

of *C. polykrikoides* may experience stress from exposures that would elicit increases in behavior to eliminate exposure, or that fish may exhibit these responses when they encounter any dinoflagellate or algal bloom. Whyte et al. (2001) observed that juvenile Atlantic salmon (*Salmo salar*) exposed to sublethal concentrations (~10 x 10^2 cells ml^{-1}) showed signs of distress (i.e. gasping and loss of equilibrium) but only 20% mortality, while at lower cell densities (~3 x 10^2) no distress and mortalities were found. Further research is clearly needed to understand the possible effects of *C. polykrikoides* blooms to fish populations. For instance, it may be possible that larval fish simply change their behavior when in a bloom of phytoplankton, whether toxic or not. Several research areas in particular seem promising for exploration in both the field and laboratory settings. These include, 1) assessing the behavior of these fish species to bloom densities of other phytoplankton species, 2) expanding on the behavioral toxicology research in this study to include a range of *C. polykrikoides* and non-toxic dinoflagellate concentrations and exposure times, 3) conducting multiple experiments for each fish species to validate results, 4) conducting avoidance experiments to determine if fish can detect and avoid *C. polykrikoides* and other HABs and at what concentrations, 5) conducting field surveys of fish populations in natural settings where these blooms are known to occur, and 6) assessing anecdotal accounts from fishermen before, during and after bloom events.

5.6 Chapter 5 Figures

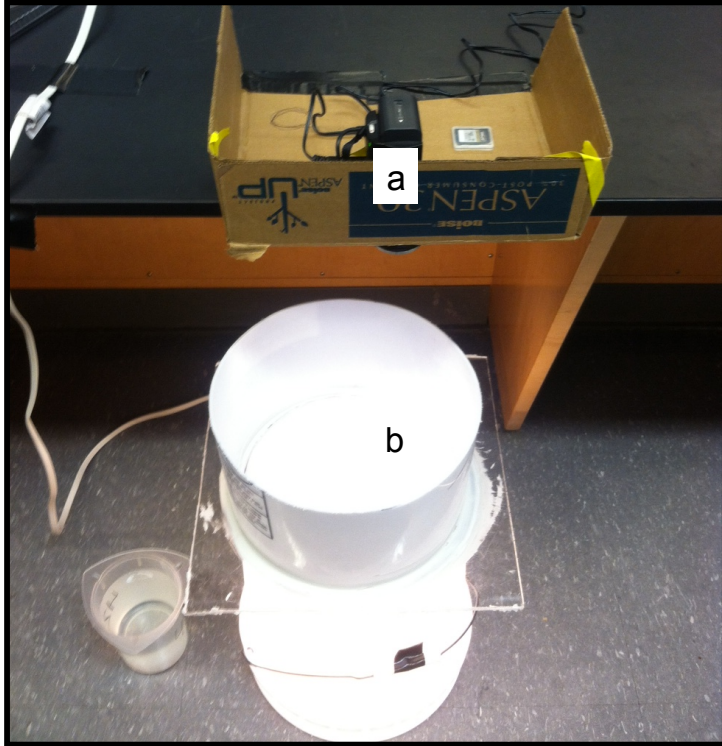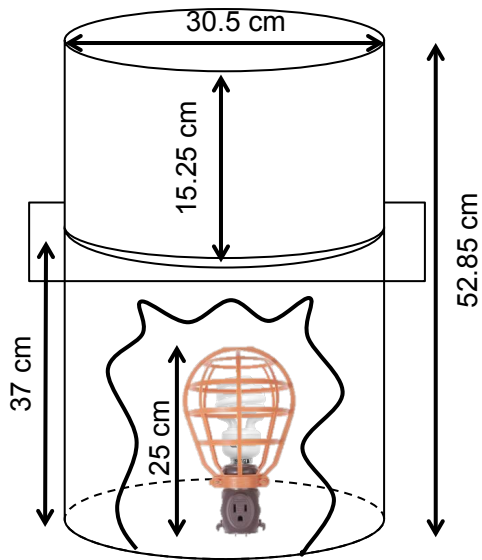Figure 5.1 Photograph of the physical design used for video experiments showing the a) video camera and b) video stage.

a) Cross-section of video stage   b) Birds-eye view of video stage
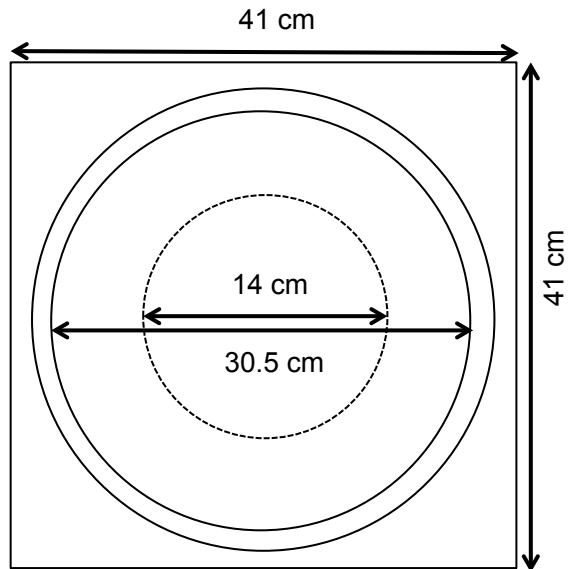
Figure 5.2 Schematic of the video stage used in behavioral experiments, showing a) cross-section and b) birds-eye vantage points. This is not drawn to scale.

Figure 5.3 Diagram of experimental procedure used in fish behavior experiments.

Figure 5.4 Box plots showing the change in a) mean swimming speed, b) mean acceleration, c) mean time active, and d) mean distance swam of Atlantic silversides between experimental and baseline portions of fish behavior trials. Treatments included a GSe culture media control and a *Cochlodinium polykrikoides* (8.5×10^2 cell ml^{-1} $\pm 1.1 \times 10^2$ SD) treatment. Lines inside box plots represent the median values, while the upper and lower segments represent the 0.75 and 0.25 quartiles respectively. Open circles represent data outliers identified by the R statistical software.
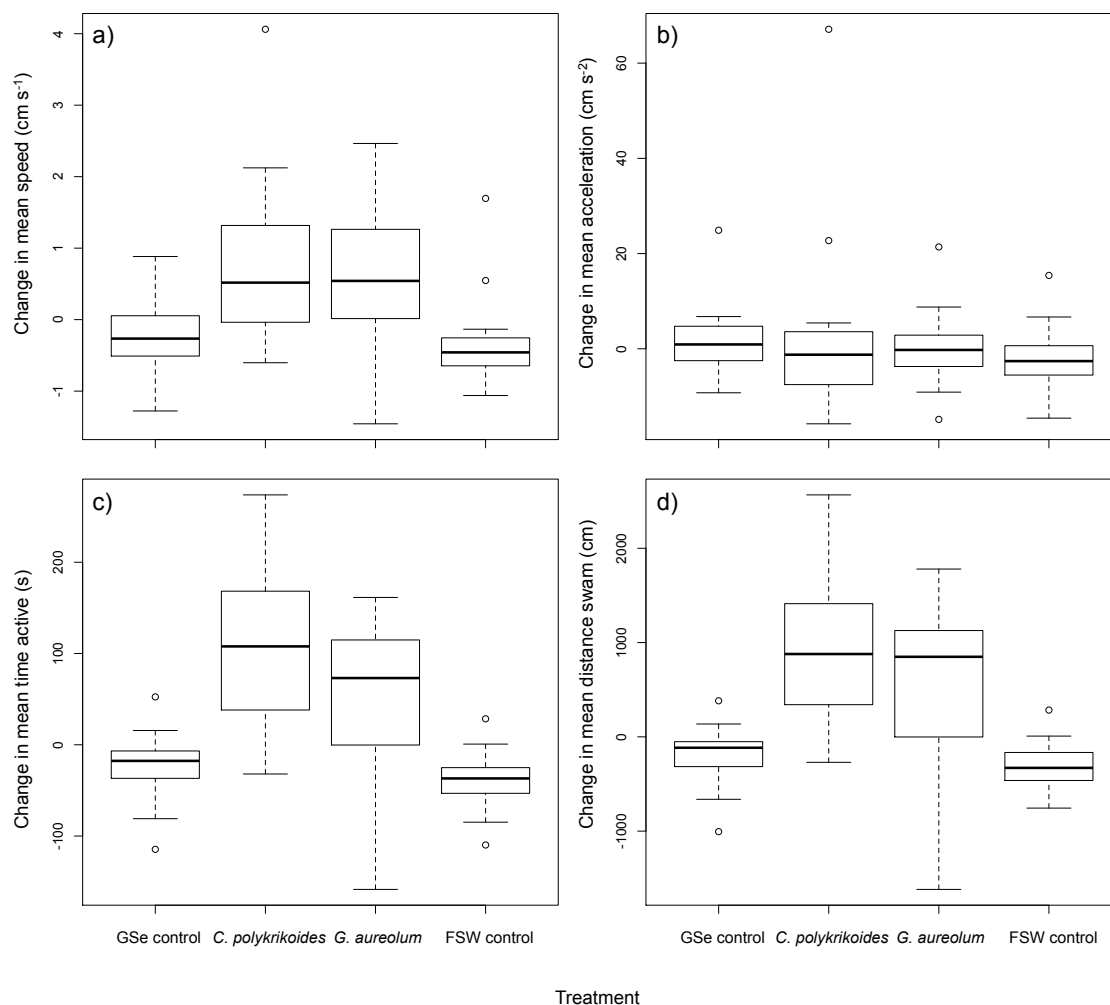
Figure 5.5 Box plots showing the change in a) mean swimming speed, b) mean acceleration, c) mean time active, and d) mean distance swam of inland silversides between experimental and baseline portions of fish behavior trials. Treatments included a GSe culture media control, Cochlodinium polykrikoides (12 x 10^2 cell ml^{-1} ±3.4 x 10^2 SD) treatment, Gymnodinium aureolum (13 x 10^2 cell ml^{-1} ±0.96 x 10^2 SD) treatment, and filtered seawater (FSW) control treatment. Lines inside box plots represent the median values, while the upper and lower segments represent the 0.75 and 0.25 quartiles respectively. Open circles represent data outliers identified by the R statistical software.
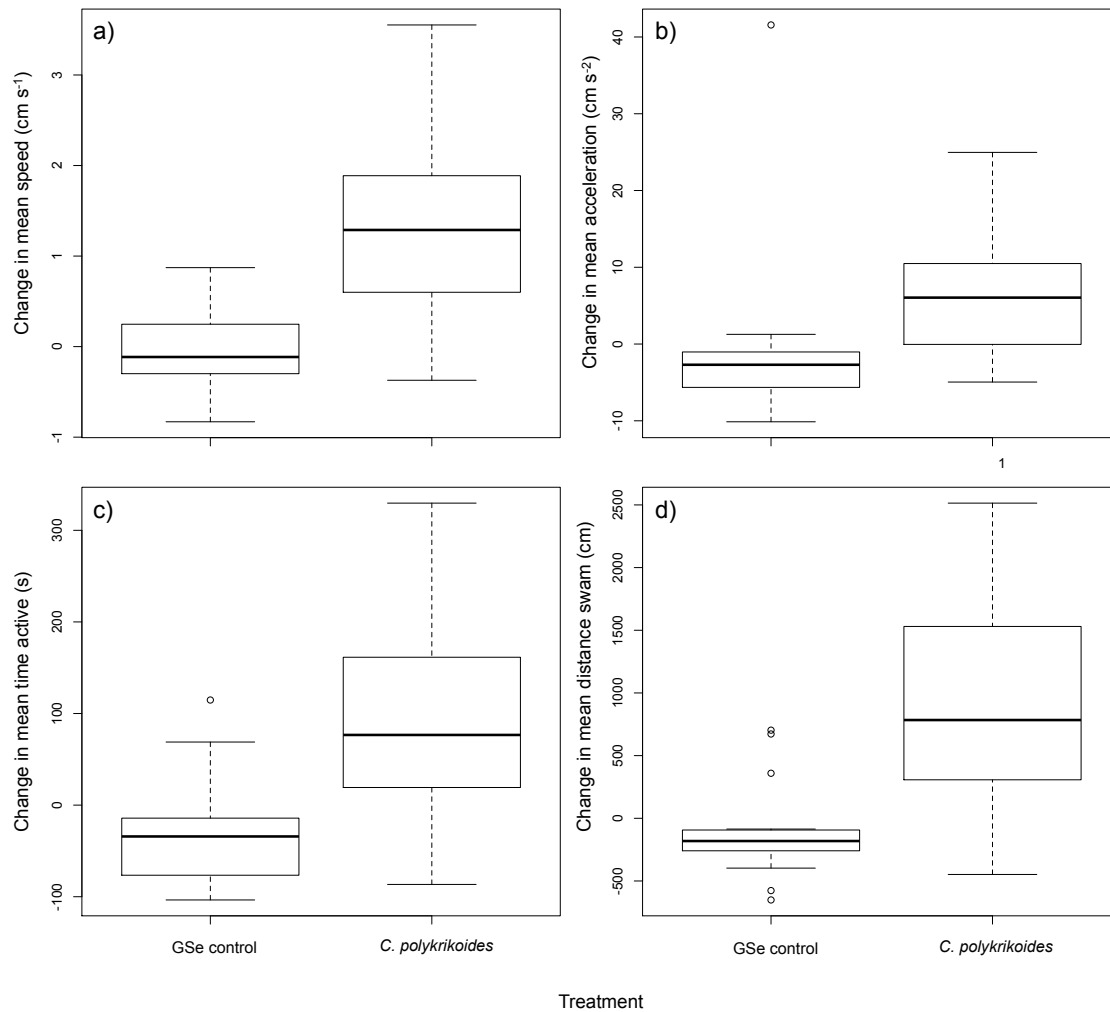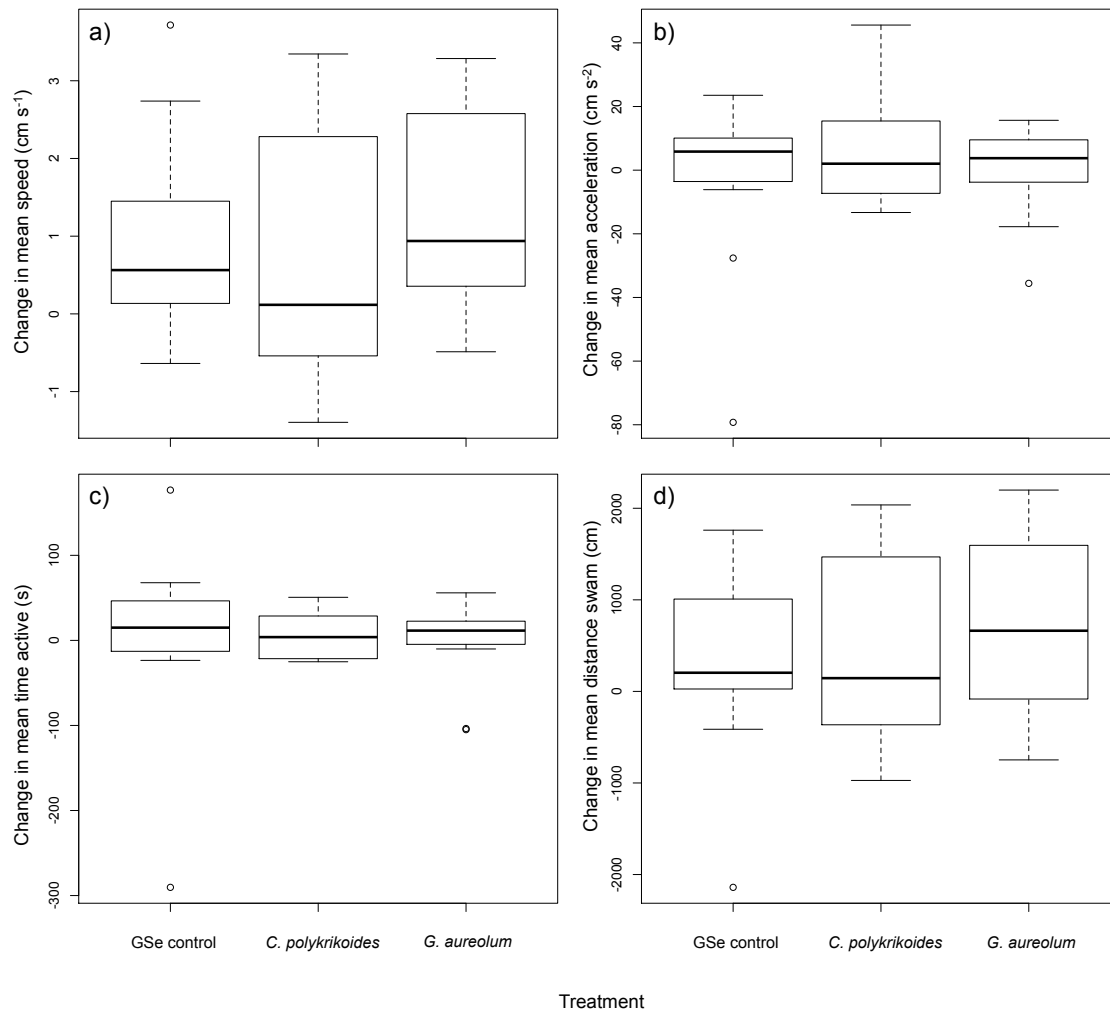
Figure 5.6 Box plots showing the change in a) mean swimming speed, b) mean acceleration, c) mean time active, and d) mean distance swam of sheepshead minnows between experimental and baseline portions of fish behavior trials. Treatments included a GSe culture media control, *Cochlodinium polykrikoides* (5.3 x 10^2 cell ml^{-1} ±0.95 x 10^2 SD) treatment and *Gymnodinium aureolum* (11 x 10^2 cell ml^{-1} ±1.1 x 10^2 SD) treatment. Lines inside box plots represent the median values, while the upper and lower segments represent the 0.75 and 0.25 quartiles respectively. Open circles represent data outliers identified by the R statistical software.

Figure 5.7 Box plots of dissolved oxygen measurements taken from fish arenas immediately after the experimental portion of each trial. Treatments included a GSe culture media control, *Cochlodinium polykrikoides* (5.3×10^2 cell ml^{-1} $\pm 0.95 \times 10^2$ SD) treatment and *Gymnodinium aureolum* (11×10^2 cell ml^{-1} $\pm 1.1 \times 10^2$ SD) treatment. Lines inside box plots represent the median values, while the upper and lower segments represent the 0.75 and 0.25 quartiles respectively.

5.7 Chapter 5 Tables

Table 5.1 Summary of behavioral experiments. Treatments included a culture medium control (GSe), filtered seawater control (FSW), non-toxic dinoflagellate control (*Gymnodinium aureolum*), and *Cochlodinium polykrikoides* clonal culture.

Species	Treatments (cells ml^{-1})	Trials	Fish arena^{-1}	Total # of fish	Mean TL (cm)	Mean mass (g)
Atlantic silverside (*Menidia menidia*)	1) GSe (0) 2) *C. polykrikoides* (8.5x10^2)	15	3	90	1.91±0.25 SD	0.03±0.02 SD
Inland silverside (*Menidia beryllina*)	1) GSe (0) 2) *C. polykrikoides* (12x10^2) 3) *G. aureolum* (13x10^2) 4) FSW (0)	15	3	180	2.09±0.31 SD	0.05±0.02 SD
Sheepshead minnow (*Cyprinodon variegatus*)	1) GSe (0) 2) *C. polykrikoides* (5.3 x10^2) 3) *G. aureolum* (11 x10^2)	12	3	108	1.97±0.28 SD	0.1±0.05 SD

Chapter 6. Conclusions

6.1 Summary of Key Findings

This dissertation has provided quantitative and qualitative insights into the contributions that forage fish species make to marine ecosystems and fisheries globally. It also evaluated the potential threats to these species arising from the geographically expanding harmful dinoflagellate, *Cochlodinium polykrikoides*. A summary of key scientific contributions from this dissertation follows.

In Chapter 2, synthesized data on forage fish species, marine predators, and fisheries, were utilized from 72 Ecopath models throughout the world. These data were linked with global catch and price databases (i.e. Watson et al. (2004) and Sumaila et al. (2007) respectively) in order to calculate the first estimates of the contributions forage fish make to the catch and catch value of commercially fished predators. This analysis demonstrated that forage fish species contributed substantially to the catches (by weight) of predatory fishes in their role as prey in many ecosystems. In terms of global catch value, forage fish were more than twice as valuable when serving as prey to predator fisheries (i.e. to tunas, cods, billfishes etc.) ($11.3 billion USD) than when directly fished ($5.6 billion USD). In addition, contrasting relationships in these values were found at latitudinal scales, with the catch value of forage fisheries being largest at the equator and diminishing poleward, while the value of forage species as prey for predator fisheries was largest at high latitudes and decreased towards the equator. Importantly, this research provided the first estimates of the contributions forage fish make in terms of biomass to: 1) the catch of predator fisheries, 2) unfished marine forage fish predators, and 3) forage fisheries. This allows for the examination of potential trade-offs between these roles across ecosystems and latitudes, as these contributions were all in the same units (Figure 2.9).

Chapter 3 focused on the role forage fish provide to marine predators, specifically seabirds, marine mammals, and large predatory bony fish. Using ecological indices calculated from a synthesis of Ecopath models, this study explored 1) the importance of forage fish species to these predators' diets, 2) their trophic characteristics, and 3) the potential for resource overlap between these predators and fisheries. The results demonstrated that forage fish are important

dietary components to many of these predators. Seabirds in upwelling ecosystems stood out in particular, as the median seabird diet consisted of 89% forage fish. In addition, seabirds, marine mammals, and large predatory bony fish generally displayed specialized feedings habits and often preferred forage fish as their most preferred prey item in the ecosystems models used in this study (Figure 3.7). Although no differences in the mean trophic levels that forage fisheries and predators were targeting at any latitude were found, potential conflicts between these groups in terms of resource overlap were low at these spatial scales. However, strong resource overlap between some predators and fisheries were found in several ecosystems in this study (e.g. seabirds in Senegambia, marine mammals in southern Benguela current, and large predatory bony fish in the northern and central Adriatic Sea, northern Humboldt current, northwestern Mediterranean Sea, and Gulf of California).

In Chapters 3 and 4, of this dissertation the toxicity of *Cochlodinium polykrikoides* to three forage fish species common to the U.S. East Coast was examined. Chapter 3 provided the first evidence of *C. polykrikoides* toxicity to early life stages of forage fish. Fish survival was generally higher amongst embryos than eleutheroembryo life stages. In addition to contributing to our overall understanding of the ecosystem effects of this harmful alga, this research demonstrated for the first time that ecologically realistic short-term exposures to *C. polykrikoides* caused significant mortality and important sublethal effects (i.e. loss of swimming) to eleutheroembryonic forage fish. Coupled with previous acute toxicological studies on larvae, juveniles and adults, these results provide information that may be useful in assessing and managing the potential population level impacts to forage fish populations in coastal areas where these blooms occur. In Chapter 4, this dissertation provided the first laboratory investigation of the behavioral toxicity of *C. polykrikoides* to larval forage fish. Larvae of Atlantic silversides and inland silversides exposed to sublethal *C. polykrikoides* concentrations displayed significantly increased swimming speeds, total time active and total distances swam compared to non-dinoflagellate controls. Sheepshead minnow larvae, however, showed no differences between all treatments. Importantly, no significant differences were found when comparing the behavioral variables from fish in *C. polykrikoides* treatments with those in the non-toxic dinoflagellate control (*G. aureolum*) treatment when they were tested. This result suggested that the changes in fish behavior observed might be due to fish encountering dinoflagellate cells, and not necessarily *C. polykrikoides* toxicity, at least at the concentrations tested in this study. This chapter

established a framework and experimental methods for future behavioral toxicity studies with *C. polykrikoides* using sophisticated video tracking software.

In conclusion, the research presented in this dissertation clearly demonstrated the importance of forage fish species at global, latitudinal, and ecosystem scales. These species make significant ecological and economic contributions to marine ecosystems and fisheries, while also facing a variety of anthropogenic threats. Forage fish species are vital dietary components to many marine predators, and were often preferred by these predators. Of the many potential threats to forage fish, this dissertation further revealed the potential consequences of a globally expanding harmful algal bloom, *Cochlodinium polykrikoides*, to their conservation.

6.2 Implications and Future Work

Forage fish species were once thought to be inexhaustible resources, largely due to their conspicuously high abundances in coastal ecosystems (McEvoy 1986, MacCall 1990, Roberts 2007). However, we now know that these species commonly exhibit unstable population dynamics, as they are sensitive to oceanographic conditions (Schwartzlose et al. 1999, Cury et al. 2000, Chavez et al. 2003, Alheit & Niquen 2004) and exploitation from fisheries (Cushing 1971, Pinsky et al. 2011). While forage fish species have traditionally been managed without explicit consideration of their ecological roles in food webs (Patterson 1992, Barange et al. 2009, Pikitch et al. 2012), there have been increased calls for an ecosystem-based approach to the management of these species. Although EBFM can be implemented from a range of knowledge about the targeted species and ecosystems (Pikitch et al. 2012), more information beyond the target species, including all interacting species, their predator-prey connections, functional responses, and population dynamics in relation to environmental and anthropogenic forces is beneficial (Brodziak & Link 2002, Pikitch et al. 2004, Richerson et al. 2010, Smith et al. 2011, Pikitch et al. 2012). These data are often sparse or unavailable in many ecosystems (Pitcher et al. 2009, Tallis et al. 2010, Bundy et al. 2012). In particular, explicit knowledge of the trade-offs between exploiting forage fish or leaving them in the water to fulfill their ecological services is crucial in EBFM of forage fish (Pikitch et al. 2012, Kaplan et al. 2013, Essington & Munch in press). This dissertation therefore provided clear implications for marine scientists, policymakers, and ecosystem managers in three major ways. First, it provided novel information on the ecological and economic importance of forage fish species to marine ecosystems and fisheries globally in

Chapter 2. Second, it provided a wealth of useable data on these contributions, predator characteristics, and ecological indices at multiple geographic scales in Chapter 3. Lastly, Chapters 4 and 5 provided new insights into the effects of *C. polykrikoides* on multiple life stages of forage fish and to their behavior. In addition to advancing understanding, this dissertation also highlighted research areas that warrant future investigation.

6.2.1 Broadening our understanding of the ecological and economic importance of forage fish globally

Synthesizing data from Ecopath models can provide many benefits for forage fisheries research as long as their limitations are understood (Pikitch et al. 2012, Essington & Plagányi 2013, Pikitch et al. 2014, Essington & Munch in press). In this dissertation, 72 and 43 Ecopath models met the requirements to be included in the analyses conducted in Chapters 2 and 3, respectively. Future syntheses could benefit by expanding in scope to utilize the nearly 500 Ecopath models that have been created (Colléter et al. 2013). This would provide improved geographic coverage and allow for increased sample sizes in future global analyses.

Although this dissertation has made significant strides in quantifying the contributions forage fish make to marine ecosystems and commercial fisheries, there were other ecological and economic contributions that fell beyond its scope. For instance, forage fish species provide a variety of other ecological services aside from their role as prey (e.g. filter filtering) that could be important. In terms of economic value, contributions that forage species make to recreational fisheries, bait fisheries, and to ecotourism could be substantial (Cisneros-Montemayor et al. 2010, Grabowski et al. 2010, Gallagher & Hammerschlag 2011, Ihde et al. 2011, Lewis 2011). In addition, forage fish reduction fisheries also stimulate the economy in ways beyond their catch value, which should be explored (Hannesson 2013, Christensen et al. 2014, Essington & Munch in press). Ultimately, comprehensive value chain analyses are needed to understand the true economic impacts forage fish make globally. The recent integration of a value chain modeling approach to Ecopath with EcoSim software may provide a useful starting point (Christensen et al. 2011, Christensen et al. 2014).

6.2.2 Comprehensive assessments of the impacts of harmful algal blooms to forage fish in marine ecosystems

This dissertation provided data from laboratory experiments that 1) filled a gap in our understanding of the effects of *C. polykrikoides* on early life stage fish and 2) provided a useful framework and methods for future behavioral toxicity studies. However, there remain several research areas that need to be explored, both in the laboratory and in the field in order for a more comprehensive understanding of the threats this HAB species poses to forage fish species and their management implications. Ideally, all of these approaches should eventually incorporate the effects of climate change and exposures to the cocktail of other anthropogenic stressors that forage fish populations face.

Future laboratory research should focus on 1) the toxinology of *C. polykrikoides*, 2) impacts to fertilization success, 3) understanding the behavioral effects of exposures to fish, and 4) assessing the potential for avoidance behavior in exposed fish. Unfortunately, there is still considerable uncertainty as to what biotoxin(s) from *C. polykrikoides* are responsible for causing fish mortality (Kim et al. 2009, Tang & Gobler 2009, Kim & Oda 2010). As recommended in Chapter 4, future toxinology bioassays should utilize early life stage fish, particularly eleutheroembryos, as they provide many benefits compared to older life stages (i.e. reduced economic costs, sample sizes, and other experimental considerations), while comparably assessing toxicity. Research could also focus on the effects of *C. polykrikoides* on the fertilization success of fish, specifically by assessing impacts to sperm motility. These impacts may be more severe than effects to individual organisms at the population level and are currently unknown. Research assessing the effects of *C. polykrikoides* on fish behavior should be expanded to test a range of cell densities over multiple exposure durations, and examine fish behavior when exposed to known prey items (i.e. *Artemia* nauplii) or other phytoplankton species. These types of experiments may help discern whether or not the behavioral responses observed in Chapter 5 were due to feeding or simply the presence of phytoplankton at bloom densities. In addition, conducting fish avoidance experiments would provide valuable insights into whether or not fish avoid ichthyotoxic alga or non-toxic species when they encounter them and at what concentrations. This information would be valuable in understanding the potential interactions between fish and phytoplankton blooms occurring in the field.

Field assessments of *C. polykrikoides* toxicity to fish are one of the least studied aspects of toxicity for this HAB species and there are many directions for future research. This

discussion is constrained to include research that will have the potential to immediately aid in ecosystem-based fisheries management. To date, field investigations of *C. polykrikoides* toxicity consisted of reported fish kills and two fish survey studies (Bauman et al. 2010, Friedland et al. 2011). Future field research should therefore focus on assessing the relative abundances and diversity of fish species at multiple life stages spatially (i.e. inside and outside of bloom patches) and temporally (i.e. before, during and after bloom events). Studies should consider sampling the ichthyoplankton community in order to assess which species of early life stage fish are exposed to these blooms (Kelso & Rutherford 1996). In addition, surveys for juvenile and adult fish should utilize standardized survey methods, whether passive (Hubert 1996), active (Hayes et al. 1996) or using acoustic gear (Brandt 1996). These surveys, coupled with laboratory experiments of fish avoidance, may be able to assess whether or not fish populations change their distribution during these bloom events, which has been previously reported by fishermen. Ultimately, elucidating the potential impacts these blooms have on fish distributions can lead to more informed decisions regarding their management (Burkholder 1998). In addition, efforts should be made to educate and enlist fishermen to collect data on their catches, so that qualitative indices of fish abundance can be made in coastal areas where these blooms occur but fisheries research is lacking.

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