Modeling in an Integrated Ecosystem Research framework to explore recruitment in Gulf of Alaska groundfish – applications to management and lessons learned

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Highlights

- Model outputs should have utility for management decisions and regional stakeholders.
- Laboratory and field data should be appropriate to inform, improve, or validate models.
- Time must be allocated to incorporate new data and mechanistic understandings into models.

ABSTRACT

The Gulf of Alaska Integrated Ecosystem Research Program (GOAIERP) supported multi-disciplinary analyses integrating physical and biological oceanography and modeling to examine how the environment influences survival and recruitment of early life stages of select commercially and ecologically important groundfish species. Recruitment is an important component of population variability, and understanding the processes influencing recruitment is central to fishery management and ecosystem planning. Determining the relative impact of advection and the environmental conditions experienced during transport between spawning and nursery areas is an inherently interdisciplinary problem. It requires consideration of physical and lower trophic level environments in concert with early life history dynamics. Here we discuss how Eulerian ecosystem models and Lagrangian Individual-Based Models for groundfish were integrated within the framework of an interdisciplinary observational program. Metrics (e.g. regionally-based averaged water temperature, integrated primary production, probability of juvenile settlement) were derived from model outputs as proxies for recruitment success. The recruitment indices were then correlated to estimated recruitment from stock assessments. Using the GOAIERP as a case study, we discuss the value that modeling can add to a field program and fisheries management planning, the challenges faced, and steps that can be taken to maximize program success. Coordination of model development, experimentation, and field sampling is necessary but can be challenging. Consideration of the appropriate sequence during data analyses and model development is critical. Careful consideration must be given to ensure that data collected in the field will inform, improve, or validate models. Sufficient time must be allocated within the program to incorporate field data collected during the program and mechanistic understandings into the models. Model outputs should be designed to have utility to management decisions and value to regional stakeholders. Collectively, the studies in this modeling program provide insight as to how models might be used to better understand recruitment processes and lead to recommendations to support the integration of ecosystem models into fisheries management.

1. Introduction

Marine fish population dynamics are responsive to environmental variation (e.g. Shelton and Mangel, 2011; Vert-pre et al., 2013; Szuwalski et al., 2015) and climate regimes (Nye et al., 2014, Barbeaux et al., 2020). However, the mechanisms influencing population variability are complicated and remain poorly understood (Rothschild, 1986; Fogarty et al., 1991; Munch et al., 2018). Determining how these mechanisms are affected by climate and fishing remains a primary objective of research to support sustainable fisheries management (Fogarty, 2014) and a critical component to effective ecosystem-based fisheries management (Link, 2002; Pikitch et al., 2004; Essington and Punt, 2011). This is particularly true for the impact of the physical environment on the biological and transport processes important to survival through the early life critical period (Hjort, 1994), and the match-mismatch in the timing of larvae and their food sources (Cushing, 1990).

1.1. Marine fish recruitment

Recruitment, or the number of new individuals joining a population each year, is an integral part of productivity and population fluctuations in marine fish. Understanding recruitment processes can inform ecosystem approaches to management. Recruitment variability, however, is poorly understood. Developing and integrating the datasets necessary to understand and predict relevant environmental influences and ecological interactions, and determining how to interpret the resulting dynamics in ways that inform stock assessments, remains a challenge.

The first weeks in life often determine survival in fish (Catalán et al., 2020). Many processes, including environmental and multispecies interactions, determine the survival or mortality of fish in this timeframe, the cumulative effects of which lead to variability in the success of annual larval cohorts. Young larval fish are typically characterized by rapid dispersal due to advection and high mortality rates due to starvation and predation. Variability in the transport of pelagic early life stages of fish to suitable nursery and settlement habitats has been at the foundation of recruitment analyses (Levin, 1994). Contributing factors to survival and mortality include fluctuations in the spatial and temporal extent, magnitude, and availability of prey fields (Okamoto et al., 2012) and predator densities (Leggett, 1986), oceanic and shelf transport (Norcross and Shaw, 1984; Fortier and Leggett, 1985; Myers and Drinkwater, 1989), and availability of suitable habitat for settlement (Wespestad et al., 2000; Johnson, 2007; Pirtle et al., 2019; Goldstein et al., 2020). In the context of fisheries management, recruitment estimation using mechanistic modeling requires determining linkages between environmental conditions and mortality estimates, understanding transport and productivity processes, identifying critical habitat, and estimating settlement rates (Houde, 1989; Chambers and Trippel, 2012; Stige et al., 2013). Beyond that, it requires determining the relative contribution of early life stages of fish to overall stock dynamics.

1.2. Fisheries management and modeling.

Fishery management aims to produce sustainable biological, social, and economic benefits from fisheries resources. This requires responding to variability and uncertainty, both in the state of the resource, the assessment of that resource, and human activity (Walters, 1986; Hilborn and Walters, 1992). Within the USA, all fish stocks of commercial importance are managed to a greater or lesser extent, with rules being implemented and enforced by governing bodies to prevent overfishing, allow for the recovery of overfished stocks, and achieve optimum yield.

Historically, fisheries management, including the annual total allowable catch, was determined solely by the estimated adult population size, with little regard to how the prevailing environmental conditions could impact survival and recruitment. Accounting for shifting distributions and changing productivity is a critical need for the development of sound scientific advice (Karp et al., 2019) for fishery management and such ecosystem considerations have been identified as a priority for the management of Alaska groundfish (Witherell et al., 2000). The USA Magnuson-Stevens Fishery Conservation and Management Act has identified the incorporation of ecosystem considerations in fisheries management to be a longstanding priority and ongoing need. To date, this has mostly been addressed in broadscale ecosystem analyses (Aydin et al., 2007; Gaichas et al., 2011; Collie et al., 2016), through the development of indirect indices or indicators of ecosystem state (Cury and Christensen, 2005; Link, 2005; Mueter et al., 2007), the application of qualitative approaches to assess ecosystem status (Mace, 2000; Zador et al., 2017), or through management strategy evaluations that include ecosystem drivers (A'mar et al., 2010; Fulton et al., 2014; Punt et al., 2016a). Progress has been made in the design of operational management strategies for achieving fishery ecosystem objectives in the face of ecosystem effects (Sainsbury et al., 2000) and in the investigation of connections between ecosystem dynamics and commercial and subsistence harvests (Haynie and Huntington, 2016). Recently, approaches have been applied to develop spatial-temporal models in ecosystem assessments (Thorson et al., 2019) and concerted efforts have been made to more explicitly link ecosystem processes directly into single-species and multispecies assessment and forecasts (Holsman et al., 2019).

It is important to determine how models fit into the management approaches currently applied when determining the utility of model products. Priorities in fishery management might be distinguished as either tactical or strategic. Tactical priorities include the development of immediate metrics, such as Overfishing Limits, Acceptable Biological Catches, and Annual Catch Limits; these might also include determining whether overfishing is occurring or if the stock is currently overfished or approaching an overfished state. Strategic issues reflect broadscale goals for how an ecosystem or a fishery might operate in the future, and include determining broad policy goals, and what control rules should be used to achieve those goals.

1.3. Integrated Ecosystem Research Programs

The North Pacific Research Board (NPRB) developed the Integrated Ecosystem Research Program (IERP) to investigate mechanistic processes that structure ecosystems, drive productivity, organize biological communities, shape species interactions and dynamics, and influence processes important to human communities and industries (Baker and Smith, 2018). Research promoted in this context is designed to advance hypothesis-driven multidisciplinary research and to promote collaboration and integration across research disciplines (e.g. field observations, laboratory investigation, and modeling) and ecosystem components (e.g. physics, fishes, humans). IERPs were implemented in the Bering Sea (BS, 2007-2012; Wiese et al., 2012), Pacific Arctic (2016-2021; Baker et al., 2020), and the Gulf of Alaska (GOA, 2010-2018; Dickson and Baker, 2016; Ormseth et al., 2019; Lindeberg et al.,2022). Common objectives of these integrated programs have been to understand the effects of climate variability and climate change on the distribution, abundance, and production of marine organisms and to incorporate this understanding into diagnostic and prognostic models that can then further inform our understanding.

1.4. Gulf of Alaska Integrated Ecosystem Research Program

The GOA (Fig. 1) is a dynamic and productive region that supports several commercially important fisheries. The international Global Oceans Ecosystem Dynamics (GLOBEC) program (Fogarty and Powell, 2002) identified the coastal GOA as one of three regions of interest in the US and established the GOA-GLOBEC program (Batchelder et al., 2005). The Gulf of Alaska IERP (GOAIERP) built on the GLOBEC effort and engaged more than 50 scientists from 11 institutions (https://www.nprb.org/gulf-of-alaska-project). This multidisciplinary project examined the oceanography, biology, and ecology of the GOA to better understand how the environment influences the survival of larval and juvenile fish to the adult stage, and ultimately the success of fisheries. Understanding recruitment variability in the GOA is made difficult by the complexity of the physical system. The strongest currents found in the Northeast Pacific flow through the GOA (Reed, 1984; Stabeno et al., 1995). This strong flow, combined with complicated topography (Zimmermann and Prescott, 2015; Baker et al., 2019) and highly variable freshwater runoff (Royer, 1982; Beamer et al., 2016; Danielson et al., 2020), contributes to a dynamic physical system which in turn influences the entire ecosystem. To identify and quantify the physical and biological factors that influence the productivity of groundfish species, five commercially and/or ecologically important groundfish species that exhibit a broad range of life history strategies were selected as the focus of the program: Walleye Pollock (WP, *Gadus chalcogrammus*), Pacific Cod (PC, *Gadus macrocephalus*), Pacific Ocean Perch (POP; *Sebastes alutus*), Sablefish (SF, *Anoplopoma fimbria),* and Arrowtooth Flounder (ATF, *Atheresthes stomias*). The suite of models developed under the GOAIERP were employed to improve understanding of recruitment fluctuations. These models covered a longer period (1996-2012) than the field sampling program (2011, 2013), and were designed to address the program's central hypothesis that early life survival is the primary factor determining the year-class strength of groundfish species in the GOA. Here we discuss 'lessons learned' from modeling within a broader integrated ecosystem research program such that our successes and shortcomings can be applied to future research efforts and further the application and integration of ecosystem modeling in fisheries management.

2. Hypotheses and approach

The GOAIERP was motivated by the foundational hypothesis that recruitment control occurs in the early life history stages (e.g. "critical period hypothesis", Hjort, 1914) and is in part driven by variation in the larval foraging environment (e.g. "match-mismatch hypothesis", Cushing, 1990). The GOAIERP proposed the following central hypothesis on survival and recruitment of five focal groundfish species:

> *The Gauntlet –*
> *The primary determinant of year-class strength for marine groundfishes in the Gulf of Alaska is early life survival. This is regulated in space and time by climate-driven variability in a biophysical gauntlet comprising offshore and nearshore habitat quality, larval and juvenile transport, and settlement into suitable demersal habitat.*

Survival of an individual fish, from spawning to recruitment, is controlled by the complex and variable biophysical environment encountered during egg and larval drift stages prior to reaching habitat suitable for juvenile settlement. This does not preclude the effect of spawning biomass on recruitment, but the working hypothesis in the GOAIERP was that post-spawning, the survival of the earliest life stages of groundfish, during transport from offshore natal areas to nearshore nursery habitats, is the principal influence affecting variability in recruitment given egg production. As such, successful recruitment may depend on many interrelated factors affecting individual fish along their transport pathways including those directly influencing survival (e.g. prey, predation), as well as those influencing the physical environment and thus the pathways themselves. We refer to the biophysical processes that occur along and influence transport pathways during the first year of life, as "*the gauntlet*".

An essential feature of the GOAIERP was its comprehensive spatial scope and multidisciplinary and integrative structure. A collaborative research approach was applied, involving four groups of scientists, three focusing on separate trophic levels (lower, middle, upper) and one constructing models (Fig. 2). Integrated physical, chemical, and biological oceanographic sampling was conducted along a comprehensive sampling grid in the GOA, extending from Baranof Island in the east to Kodiak Island in the west (Fig. 1). Ecosystem surveys were conducted at inshore and offshore sites and field surveys were complemented by laboratory analysis of food habits and energetic condition, physiological experiments, and modeling. Environmental conditions and processes influencing early ontogenetic stages of the focal fish species were examined (Doyle and Mier, 2015), and results were used to develop species-specific individual-based models (IBMs) to predict recruitment variability under various environmental scenarios (Fig. 3; Gibson et al., 2019, Stockhausen et al., 2019a, 2019b, Hinckley et al., 2019). Discussions before the start of the GOAIERP program conceptualized the likely connections between model results and field data. Research design, data collection, analysis, and interpretation were closely coordinated among the groups beginning early in the research design phase.

To address the overarching gauntlet hypothesis and assess the impact of environmental variability in driving transport and success of early life stages from spawning to settlement, the GOAIERP modeling group integrated a series of modeling tools to address the following specific hypotheses:

> H1: *Recruitment variability of the five focal species is primarily influenced by variability in the proportion of young fish transported from offshore spawning areas to nearshore nursery areas (connectivity) due to interannual differences in the strengths of the physical regimes that characterize the GOA environment.*
>
> H2: *Recruitment variability is (secondarily) influenced by the survival of young fish successfully transported to nursery areas, which varies due to differences in physical factors (wind speed and direction, water temperature, runoff, mixing) and biological processes (prey abundance, competition, predation) encountered along the transport pathways.*

3. Species-specific Individual-Based Models

The suite of models to test H1 and H2 included a physical oceanographic model that simulated the ocean environment, a lower trophic level model that simulated nutrients, phytoplankton, zooplankton, production, and biomass fields, and early life history models for each of the five focal species. Each of the GOAIERP models has been previously described in detail but is summarized below.

3.1. Eulerian physical oceanographic and lower trophic level models

The well-established Regional Ocean Modeling System (ROMS, Haidvogel et al., 2008; Moore et al., 2004; Shchepetkin and McWilliams, 2005) was used to simulate the time-varying, three-dimensional hydrodynamics in the GOA. The implementation of ROMS for the GOA has a horizontal resolution of approximately 3 km and can replicate common features in GOA circulation that can influence transport—such as currents, eddies, meanders, and hydrographic fronts (Cheng et al., 2012; Coyle et al., 2013; Dobbins et al., 2009; Hermann et al., 2016, 2009a; Hinckley et al., 2009a). A lower trophic level Nutrient-Phytoplankton-Zooplankton (NPZ) model was also developed and validated for the GOA (Hinckley et al., 2009b; Coyle et al., 2012, 2013) and includes nitrate, ammonium, iron, large and small phytoplankton, microzooplankton, large and small copepods, and euphausiid components (Fig. 4). The NPZ model was fully integrated within the ROMS framework and the coupled model was run for 1996-2011 providing a 16-year time series of model output for driving the IBMs.

3.2. Lagrangian larval fish models

Spatially explicit biophysical IBMs that use Lagrangian particle tracking algorithms have been widely applied to study recruitment (e.g. Hinckley et al., 1996; Stockhausen and Lipcius, 2003) and connectivity (e.g. Cowen et al., 2006, 2007). Each IBM used in the GOAIERP (Fig. 3) was developed to reflect early life characteristics and behavior for the focal groundfish species. They integrated biological processes affecting simulated individuals as they develop in time through multiple early life stages, as well as due to advective and diffusive transport. The WP model was developed under past research efforts (Parada et al., 2016, Hinckley et al., 2016) using the Ichthyop 3.1 framework (Lett et al., 2008), while the remaining four IBMs were developed within the GOAIERP (Gibson et al., 2019; Stockhausen et al., 2019a, 2019b, Hinckley et al., 2019) using the Dispersal Model for Early Life Stages (DisMELS; Stockhausen, 2021) framework. Both IBM platforms used stored oceanographic and lower trophic level output from the coupled ROMS-NPZ model to simulate the environment experienced by early life stages. The IBMs were synthetic and integrative, incorporating data obtained during and prior to the GOAIERP.

ATF, SF, and POP spawn in deep water at the edge of the continental shelf in the GOA. In contrast, WP spawn primarily in Shelikof Strait while PC spawn on the GOA continental shelf. The deep spawning species utilize shallow inshore habitats as juvenile nursery areas while juvenile WP and PC can be found across the shelf. Each species-specific IBM was informed by a conceptual model of its early life history (Fig. 3). The degree of complexity in each IBM reflected the data available for each species. For example, pollock has historically been well studied in the GOA so information on spatially explicit annual spawning biomass and predation pressure was available for it, but not for the other focal species. A brief description of the early life history for each species is outlined below and a summary of each life stage and the key model features are shown in Table 1.

Tens of thousands of individual model fish were released in each simulation and each IBM was run annually from spawning (first life stage is eggs) through to ‘settlement’, or the end of the year. To support subsequent examination of individual histories, the entire history for each individual ‘fish’ was retained on a daily time interval (i.e. location, depth, length, age, life stage), along with information on their physical (i.e. temperature) and biological surroundings (i.e. biomass of zooplankton prey fields) from the ROMS-NPZ model.

Walleye Pollock (WP)

WP are very fecund with highly variable mortality and growth rates in early life. Eggs are released at 200-300 m depth in March and April and hatch two weeks later. Larvae begin diel migration when they are ~7 mm in size, and gradually increase their swimming capacities until their movement becomes independent of currents (Fig. 3a). Optimal WP prey depends on larval size, temperature, light, turbulence, and turbidity (Porter et al., 2005). Predation on juvenile WP may be important to recruitment, particularly as groundfish predator abundance has increased since the 1980s. Environmental effects on larval survival were key to recruitment success prior to the increase in predator biomass (Bailey, 2000). The prevailing hypothesis for WP is that Shelikof Strait comprises the primary spawning area and the Shumagin Islands are the main nursery area (Hinckley et al., 2001). Currents transport larvae southwest along the Alaska Peninsula (Yoklavich and Bailey, 1990; Hinckley et al., 2001). The IBM for WP included four life stages (egg, yolk-sac larvae, feeding larvae, and age-0 juveniles. Egg development was driven by age and temperature, growth of yolk-sac larvae depended on degree days, the growth of feeding larvae and juveniles depended on consumption estimated as a function of individual weight and temperature, and predation on juveniles was based on groundfish predation data (Megrey and Hinckley, 2001; Parada et al., 2016).

Pacific Cod (PC)

PC spawn between February and July in the GOA (Dunn and Matarese, 1987) over rocky substrates at depths of 20-200 m (Hurst et al., 2009). Egg and larval dispersal may be limited because eggs are demersal, and semi-adhesive (Alderdice and Forrester, 1971). Hatching of pelagic yolk-sac larvae at ~3-4 mm standard length (SL) 21-26 days after fertilization and individuals show strong surface orientation (Hurst et al., 2009). Juvenile nursery areas are primarily shallow, coastal embayments (Abookire et al., 2007; Laurel et al., 2009). The IBM for PC included six stages (egg, yolk-sac larvae, pre-flexion feeding larvae, post-flexion feeding larvae, epipelagic juveniles, and settled juveniles), with stage-specific processes modeled for growth, development, depth distribution, and diel migration (Hinckley et al., 2019; Fig 3b).

Pacific Ocean Perch (POP)

POP are members of the *Sebastes* genus, a primitive viviparous group (Love et al., 2002). Reproduction occurs in April-May (Westerheim 1975) at depth (500-700 m). Larvae remain at depth for a month or more, before moving to shallower depths (Love et al., 2002). They begin feeding at 3-7 mm SL (Kendall and Lenarz 1987) and occupy the near-surface layers. The duration of the larval stage is 1-2 months (Matarese et al., 2003) and this stage completes at 20-30 mm SL. POP juveniles in the GOA remain in the water column for several months until fall, at which time they use demersal subtidal habitats with complex topography and extensive cover (Carlson and Haight, 1976). The IBM for POP consisted of five sequential early life stages: preflexion larva, postflexion larva, pelagic juvenile, settlement-stage juvenile, and benthic juvenile (Fig. 3c). The first four stages were defined in the IBM to facilitate ontogenetic changes in "preferred" depth ranges, growth rates, and movement parameters. The final stage (benthic juvenile) was simply a "marker" that indicated an individual had successfully settled in a benthic nursery area. The IBM did not include bioenergetics or directed swimming. Similar to PC, the GOA model domain was divided into 12 alongshore zones and several depth zones for analysis.

Sablefish (SF)

SF spawn pelagic eggs in winter near the edge of the continental shelf (Kendall and Matarese, 1987), with peak egg abundance in the western GOA in February (Doyle and Mier, 2015). Eggs are found at depths >200 m and require 2-3 weeks to hatch (Mason, et al., 1983). Before hatching, eggs sink to depths exceeding 400-500 m and maintain that position. The time from hatch to first feeding is around two weeks (Boehlert and Yaklovich, 1985). Once the yolk sac is absorbed, larvae swim to the surface and grow about 2 mm per day from about 10 to 80 mm SL (Kendall and Matarese, 1987; Shenker and Olla, 1986). Following the transition to the juvenile stage, individuals continue to inhabit the upper water column but undertake diel vertical migrations, moving higher in the water column at night (Courtney and Rutecki, 2011; Sogard and Olla, 1998).

The IBM for sablefish included five sequential early life stages: egg, yolk sac larvae, feeding larva, epipelagic juvenile, and settlement-stage juvenile (Fig. 3d). Each life stage was parametrized with different growth rates, depth preferences, vertical swimming speeds, minimum and maximum stage duration, and minimum size for stage transition.

Arrowtooth Flounder (ATF)

ATF spawn along the continental slope at depths of 100-500 m (Blood et al., 2007). Spawning begins in December (Blood et al., 2007). Eggs are pelagic and the duration of the egg stage is temperature-dependent. The mean size at hatching is 4.4 mm SL (Blood et al., 2007) and yolk absorption is complete by 6.5-7 mm SL. Flexion occurs at 13.4 mm SL and transformation occurs at 45 mm SL (Blood et al., 2007, Bouwens et al., 1999). Larvae ascend to shallower depths before yolk sac absorption is complete. While most larvae are found along the outer shelf and slope, many late-stage eggs and larger larvae have been found farther inshore and associated with troughs and canyons, where downwelling relaxation and cross-shelf flow occur (Bailey and Picquelle, 2002). Interannual variation in size is small compared to intra-annual variation, suggesting that arrowtooth flounder hatch over an extended period (Bouwens et al., 1999). Settlement begins in early August and finishes by the end of October. The IBM for ATF was relatively simple, reflecting the limited knowledge of the early life stages for this species. Growth rates were stage-dependent and movement was passive and undirected, except that individuals moved vertically to remain within stage-specific “preferred” depth ranges. The model used eight sequential early life stages: egg, small yolk sac larva, large yolk sac larva, small feeding preflexion larvae, large feeding preflexion larvae, postflexion larvae, settlement-stage juveniles, and benthic juveniles (Fig. 3e).

4. Analytical approach and result highlights

Several research questions (summarized in Table 2) were developed in discussions between the four GOAIERP research groups early in the program. These were then clarified as specific analyses that might be applied to address the primary hypothesis. Modeling hypothesis H1 was addressed for all five focal species by performing connectivity analysis between spawning and nursery areas. Hypothesis H2 was addressed through analysis of individual trajectories and histories that provide details of the ‘gauntlet’ experienced during the first year of life as the young fish were transported from offshore spawning areas to nearshore nursery areas. Because the IBMs were of varying levels of complexity, depending on the information available to construct them, we were able to apply the various types of trajectory analyses in more depth to some species than others. Each type of analysis performed is outlined below and example results are provided.

4.1. Connectivity analysis

Population connectivity, i.e. the relative strength in connectivity between each spawning and nursery area (e.g. successful endpoint), is inherently a coupled bio-physical process and research topic, involving physical processes (e.g. eddies, fronts, tides, geomorphology; Cowen and Spounagle, 2009), as well as biological processes including behavior (e.g. vertical migration; Cowen et al., 2002). The working theory for the connectivity analyses was that physical properties are important in driving the size of the annual recruitment to the fishery (i.e. H1). The strength of connectivity between areas is often expressed as the proportion of individuals released from a spawning area that settled into a suitable nursery area, such that it is independent of spawning stock size (Gibson et al., 2019; Stockhausen et al., 2019a). Connectivity can be impacted by the simultaneous and combined effects of individual movement and physical forcing (e.g. currents).

The IBMs for PC, ATF, SF, and POP divided the GOA model domain into 12 alongshore spawning and nursery zones (Fig. 5a), and several species-dependent depth zones. The GOA model domain for WP was split into 45 bathymetric and topographically defined areas, allowing a more detailed analysis. Connectivity values were calculated and analyzed at the end of each simulation year for each spawning area-nursery area pair to develop a series of connectivity matrices summarizing the interannual and median connectivity across the GOA for all species. This allowed an examination of the interannual variability in “total connectivity”, the sum of all probabilities in the connectivity matrix for each year, as well as the interannual variability in connectivity between known/likely spawning and nursery areas. Connectivity indices were subsequently correlated with stock assessment recruitment estimates (see section 5).

Mortality processes along individual trajectories were not estimated or included except for WP. “Connectivity” therefore represents “maximum potential” connectivity between each spawning and nursery area (i.e. Fig. 5) due to the interaction of physics and basic life history dynamics. Understanding the connectivity between spawning and nursery areas in our study domain enabled the identification of key spawning and recruitment sites for each species and quantification of the degree to which physics alone can account for observed transport to nursery areas. For example, results from the Sablefish IBM indicate that, in the absence of directed horizontal movement, sablefish spawned throughout the GOA have the highest probability for settlement in nursery areas in the central GOA (Fig. 5b). However, near-shore waters extending from southeast Alaska to British Columbia are known to be some of the most important nursery grounds for young sablefish (Sasaki, 1985), and juvenile sablefish are found consistently only within St. John Baptist Bay (Fig. 1; Rutecki and Varosi, 1997). The probability of connectivity to this region is not particularly high if spawning is assumed to occur evenly along the shelf break throughout the GOA. This supports the hypothesis that sablefish spawning is likely more concentrated in areas in the southeast GOA, or that settlement to this region depends on selective behavioral traits of young sablefish not presently captured in the model. The spawning-nursery area connectivity pattern for ATF (Fig. 5c) was similar to SF with a general east to west connectivity and the highest probability for settlement in nursery areas in the central GOA.

The results of modelled connectivity patterns indicate that the early life history stages of PC generally do not disperse far from their natal areas (Fig. 5d). Retention of modelled individuals in areas where they were spawned was the strongest connectivity pattern seen.

4.2. Trajectory analysis

Contrasting the route taken by ‘successful’ individuals (i.e. those that reached a nursery area) and ‘unsuccessful’ individuals (i.e. those that failed to) is useful in understanding what physical or biological factors could make the difference in successful recruitment. Differences in the biotic and abiotic environment experienced along individual trajectories throughout the simulation were contrasted between successful recruits and non-settlers. Trajectory analysis undertaken included (1) physical processes (e.g. eddies, currents) that directed fish towards or away from favored nursery areas; (2) topographic features that influenced trajectories; (3) temperature histories of successful settlers and non-settlers; (4) optimal duration of the pelagic stage; and (5) correlations between successful settlement and movement over viable habitat.

4.2.1. Visualizing individual paths

Visually examining trajectories of individuals within the model grid can be considered the most basic form of trajectory analysis, but large number of simulated individuals made it hard to discern useful information. Displaying individual trajectories for only certain spawning/natal areas, or individuals of a certain life stage was more informative (i.e. Stockhausen et al., 2019a; 2019b).

The difficulty in disentangling ‘spaghetti’ plots led to the development of a ‘mean trajectory’ from each spawning area to reveal the path individuals took on average. Visual examination of trajectories identified notable interannual differences in transport, for example, in the numbers of young ATF carried offshore in large oceanic eddies (Stockhausen, 2019a); while some of these fish returned to the shelf, many failed to reach a suitable nursery area and were considered unsuccessful and lost to the system.

Visual inspection showed that while most of the individuals that exited the GOA model domain did so along its western edge. Some individuals exited the grid to the southeast (Stockhausen et al., 2019b; Gibson et al., 2019), which is somewhat counterintuitive as the dominant flow in the GOA is counter-clockwise. These individuals were transported in this direction by ephemeral mesoscale processes, such as wind-driven currents, at the edge of the model domain. Visual inspection of WP trajectories allowed an exploration of the transport from known spawning areas in the GOA to nursery grounds. From the Cook Inlet spawning area. individual particles were transported to Shelikof and Semidi islands region where juvenile aggregations have been observed (Fig. 6ai; Wilson et al., 1996). In contrast, the East Kodiak Island spawning region produced trajectories that entrained individuals into mesoscale eddies off the shelf (Fig. 6aii) while the Shelikof Strait spawning area produced individual trajectories that connected to the Shumagin Islands region, a known nursery ground for WP (Fig. 6aiii).

4.2.2. Path analysis

“Path Analysis” was performed to search for common trajectories or areas of the GOA used heavily by the focal species. For each year, individuals were grouped by spawning area and recruitment status (successful/unsuccessful), and trajectories were examined to determine which grid cell each particle was in at each time step. All instances of a particle being in a cell were tallied (considering particles that were retained in the cell and those that entered or left the cell) to derive a ‘particle day count’ for each grid cell that showed common routes or retention regions for particles. The results were used to see if the transport of individuals was notably different in low and high recruitment years. For example, the path analysis for sablefish spawned in the southeast GOA indicates that in a high recruitment year (2000), individuals were initially retained close to the shelf break in what appears to be a small eddy (Fig 6bi) and the common successful path seems to be moving onto the shelf early, just north of Baranof Island. Conversely, in a lower recruitment year (2011) most individuals appear to be retained, at least for some time, in a large eddy that transported them off-shore (Fig. 6bii). The Path Analysis did not show individual transport routes, but instead showed a pattern of use of the shelf. It also showed, as did the visual inspection of trajectories, that some settlers could be transported quite far offshore and still return and settle. This would appear to indicate that entrainment in the Alaska Stream or the large mesoscale eddies is not necessarily fatal, assuming a sufficient food supply in these eddies. Visual inspection and the path analysis of PC trajectories showed that Amatuli Trough could act as a transport pathway off the shelf when fish were in the top 20 m of the water column. Often the Amatuli Trough is thought of as a means for early life stages of some species located deeper in the water column to transit from deep slope or oceanic areas up onto the continental shelf (Mordy et al., 2019). Our finding underscores the importance of differences in the life histories of the focal species. An overlap coefficient (*OC*; Hinckley et al., 2016) was used to quantify the overlap of path analysis matrices in low, median, and high recruitment years (i.e. Hinckley et al., 2019).

4.2.3. Tortuosity Index

Computation of a “Tortuosity Index” for trajectories allowed examination of their twistiness, or tortuosity, to determine how direct a route each individual took, as it was transported to (or away from) nursery areas. We defined tortuosity as the arc-chord ratio, the ratio of the total length of the trajectory (actual distance traveled), to the direct distance between the endpoints (i.e. spawning and settlement location). This index was computed for each individual in each group and then averaged over spawning groups and recruitment status (e.g. successful, unsuccessful). The tortuosity analysis for WP showed the most convoluted trajectories occurred in 2002, indicating that in this year the trajectory paths were much longer than the straight-line distance between starting and ending points. A reduction in tortuosity was observed from 2005 to a minimum in 2008. Examples of more tortuous and less tortuous trajectory indices are shown in Fig. 7.

4.3. Summarizing the biophysical experience

Environmental conditions could facilitate or impede groundfish transport, development, and successful recruitment. To address H2, i.e. that recruitment variability is influenced by the survival of individuals as they are transported from spawning to nursery areas, we developed a series of environmental indices. Indices representing large-scale environmental processes in the North Pacific Ocean and GOA (i.e. the Arctic Oscillation and the Pacific Decadal Oscillation) were considered, as were more regional scale (i.e. eastern/western onshore/offshore) indices developed directly from the GOA ROMS-NPZ model. Other environmental indices were developed from IBM trajectory analysis summarizing the environment directly experienced by each individual. Environmental variables considered included regionally-averaged upper water-column salinity and temperature, integrated primary production, cross-shelf flow, temperature and salinity along the trajectory, zooplankton biomass encountered, life-stage pelagic duration, and days spent over suitable settlement habitat. As was the case with the connectivity and trajectory path analysis, each environment index was expressed on an annual time scale so that they could be correlated to stock assessment measures of recruitment (see section 5). Environmental conditions for individuals spawned in different areas were often highly correlated. For example, 2002 was colder and more saline for all SF individuals regardless of where they were spawned (Fig. 8). Similarly, the Degree Days index calculated for PC trajectories, which summed temperature at each location for each day over the entire trajectory, found the temperature experienced by settlers and non-settlers to be similar, suggesting that experienced temperature was not a direct determinant of survival to settlement.

For WP, the different conditions encountered by successful and unsuccessful individuals were further explored using a multivariate Empirical Orthogonal Functions (EOF) analysis performed on the normalized (z-score) values of environmental variables encountered along each trajectory during the year 2008. While a typical physical EOF would look for the spatial structure of a *single* variable on a grid, multivariate EOFs (individual/variable/time) were used to explore coupled biophysical modes that varied through time across individual trajectories. The environmental experience between those individuals that successfully recruited to the nursery areas (“winners”; Fig. 9a) versus those who were unsuccessful, i.e. those that did not settle, or exited the grid (“losers”; Fig. 9b) was then compared. The goal was to seek out characteristic life histories that lead to a winning or losing result. The results of the formal EOF analysis and environmental indices suggest that there are more ways to “win” than to “lose” (Fig. 10). The two dominant factors (1st and 2nd mode of the EOF analysis) have time amplitudes that explain life history changes during different parts of the year. The first mode has a modest negative amplitude followed by an abrupt change near late July - early August, while the second mode has a gradual negative to positive trend from spring into summer, followed by a decline to zero amplitude in the fall. Overall, the second mode explained most of the collective variance across individuals and their sampled environment in the summer, while the first mode explains most of that collective variance in the fall. The sharp change in amplitudes in early fall is a natural consequence of the dramatic change at that time in several of the included variables (e.g. neocalanus and life stage). In both modes, the individual ‘winners’ exhibit a broad range of loadings on any life history variable (not shown), and the near-zero average of loadings for each biophysical variable over all those winning individuals (Fig. 10 c,d) indicates no characteristic pattern of winning life history. This indicates that each individual has experienced a rather unique sequence of life history events (e.g. food, temperature, depth) on their way to settlement. Conversely, the losers tend to have similar loadings on any particular variable; averaging over losing individuals reveals common features of their life histories (Fig. 10 e,f). This averaging reveals that losing individuals are gradually advected into deeper areas over the spring and summer (note the strong positive loadings on bathymetry and the positive trend through time) and experience lower values of temperature, euphausiids, and copepods and higher values of salinity (consistent with offshore conditions) in the fall.

5. Using GOAIERP models to predict recruitment

5.1 Correlating model indices with recruitment

We computed the Pearson's correlation coefficient (Table 3) between our indices (computed for 1996-2011) and the stock assessment estimates of recruitment (A'mar and Palsson. 2014; Dorn et al., 2016; Hanselman et al., 2016; Spies et al., 2016; Hulson et al., 2015) to determine which of the annual indices from our connectivity, trajectory, and environmental analysis might be important to understanding and predicting the recruitment of groundfish. For some species, the analysis was extended beyond simple correlation to involve linear models that combined multiple connectivity and environmental indices and had greater explanatory power. Correlations between the time series (1996-2011) of percent of individuals settled in each nursery area derived from the PC connectivity analyses showed that the fraction settled in the Shumagin Island was positively correlated with observed PC recruitment, indicating that this may be an important nursery area. Settlement in this region was positively correlated with the North Pacific Index (NPI) (r=0.53, p<0.05) and negatively correlated (r=-0.54, p<0.05) with the Multivariate ENSO Index (MEI). This indicates that PC success in settlement and recruitment may be increased when the GOA gyre circulation is low, enhancing retention and short-distance transport, and minimizing transport out of the GOA. For PC, the Degree Days index for the individuals that exited the GOA was significantly negatively correlated with normalized PC recruitment (A'mar and Palsson, 2014). Also for PC, the Tortuosity Index for settlers was significantly positively correlated with recruitment. These indices also show that restricted transport of early stages is important.

The total annual connectivity between all spawning and nursery areas for SF was positively correlated to recruitment (r=0.45, p=0.08). The strongest correlation (r=0.56, p<0.05) to SF recruitment estimates was with the cross-shelf flow index. The tortuosity index generated using the WP IBM output showed an inverse relationship with recruitment (r=-0.42, p=0.11). This implied that more direct trajectories led to higher recruitment and that recruitment is positively affected by efficient transport to nursery areas.

While the identification of indices to reliably predict recruitment in isolation has proven elusive, these analyses have identified consistent mechanisms that may underlie successful recruitment. Submesoscale eddies might play a role by concentrating or dispersing food availability in some areas and affecting the direct arrival to potential nursery areas. These results also present new hypotheses that should be tested in future research efforts.

5.2. Models for mechanistic understanding vs. recruitment prediction tools

Using ecosystem models and IBMs as recruitment prediction tools to inform stock assessment presents several challenges but is a worthy goal. IBMs do not directly predict recruitment, rather they predict indictors for potential recruitment (e.g. the probability that individuals will be successfully transported to a suitable nursery ground). Delivery to suitable nursery habitats is necessary, but not sufficient for recruitment. A more realistic strategy for IBM integration into stock assessments is to incorporate the strength of correlations between model predictions and past empirical observations of recruitment (Kough et al., 2013). De Oliveira and Butterworth (2005) suggest that recruitment indices from an IBM can be considered useful for management if the index, or combination of indices, can explain >50% of the variability in past recruitment. While we were able to achieve this goal for some of our focal species, such as POP (Stockhausen et al., 2019), sablefish (Gibson et al., 2019), and PC (Hinckley et al., 2019), we argue that the true value of an IBM to both assessment scientists and fisheries managers lies in its ability to compare the relative importance of potential mechanisms underlying recruitment variability (i.e. to suggest *why* a correlation might be evident). This type of approach helps to narrow the range of potential environmental predictors for each species (Table 3).

Insights from the GOAIERP as to how recruitment is affected by environmental conditions and the spatial relationships between spawning and nursery grounds may improve future estimates of stock structure and essential habitat. Our findings also might contribute to the development of appropriate ecosystem-based management schemes when planning for future climate regimes. For example, an IBM could provide the basis for environmentally-forced recruitment for a Management Strategy Evaluation (MSE; Punt et al., 2016b), with candidate management strategies evaluated against each other based on responses to a set of hypothesized environmentally-linked recruitment regimes provided by the IBM.

*5.3 Model results to explore short-term impacts and long-term projection*s

Managers are interested in not only the short-term recruitment potential of a stock, but the stock response to climate variability, climate change, and regime shifts. As part of the Intergovernmental Panel on Climate Change Fifth Assessment Report (AR5, IPCC 2013), global forecasts have been developed and used to explore the coupled global atmospheric and oceanic response to anticipated changes in atmospheric CO_2. It is relatively common to see these long-range forecasts used to drive regional biophysical models to quantify expected changes in ocean productivity. While this approach has utility in understanding the physical response of the ocean and lower-trophic level organisms, its utility lessens as we consider organisms with more complex lifecycles and behavioral responses. Furthermore, while the IPCC predictions generally agree that there will be warming over the next 50 years, salinity, not temperature is the dominant driver in the GOA. This region has a very narrow continental shelf bordered by steep glacial mountains thus the variability in freshwater runoff is highly influential (impacting the buoyancy-driven Alaska coastal current, water column stability and mixing, and shelf/ocean exchange (Royer 1982,1998; Hill et al., 2015). It has been postulated that the IPCC models generally do a relatively poor job of mimicking the freshwater inputs (Stabeno, NOAA-AFSC, pers. comm.). We do not believe that recruitment predictions using these long-range predictions of forcing will have strong predictive power for GOA fisheries because freshwater is essential to understanding the physical, and therefore the biological, dynamics of the GOA. The approach taken within the framework of the GOAIERP (i.e. development of recruitment indices for focal species and attempting to understand the recruitment response and underlying mechanisms of each species to any given physical regime), is a more robust strategy and more likely to produce useful results that could inform the adaptation of management schemes within the context of regime shifts.

5.4. Linking spatial model outputs to systemwide recruitment

A key result of the GOAIERP has been to describe the diversity of processes in the GOA, especially the formal recognition of distinct dynamics in east and west (Zador and Yasumiishi, 2016) and connectivity between domains (Goldstein et al., 2019; Siddon et al., 2019). These domains represent diverse user communities with different concerns and priorities. A “whole region" model, such as a stock assessment or bulk biomass (non-spatial) food web model, may be limited in its ability to deal with spatial structure, especially if links between east and west vary over time.

An important part of management for some wide-ranging stocks in the GOA (e.g. SF) is area apportionment of fishing quotas. To this end, the most management-useful recruitment indices derivable from IBMs may not predict absolute recruitment, but rather spatially-relative recruitment, how strongly east and west are coupled, or the connection into/out of the GOA, and whether these change over time. IBMs are uniquely suited to produce such spatially derived indices, or for producing spatial recruitment estimates for seeding a spatial whole-ecosystem model.

5.5. The effects of the five focal species on the food web

To bridge the gap between the ROMS-NPZ-IBM modeling efforts and management of fisheries in the GOA, we initially proposed to incorporate our indices into an Ecosim food web model of the western GOA (Gaichas et al., 2010, 2011). The NPZ components and five focal fish species of GOAIERP are directly connected by the distance of single predator/prey links to almost all the 124 functional groups in the Ecosim model (Fig. 11), showing the central role of the focal species in the ecosystem.

The food web model can be used to show the sensitivity of the food web to variability in the biomass of the focal groundfish species, as well as explore uncertainties in our current knowledge, and inform prediction, particularly in recruitment. Through a series of simulations with the food web model, we lowered the recruitment production of each of the focal species by 10%, in turn, and simulated the new ecosystem state resulting from the perturbation. Monte Carlo sampling was used to generate a range of potential ecosystems within the error bounds of the input parameters (biomass and diets). WP and ATF had substantial ecosystem impacts (Fig. 12), while PC, POP, and SF led to fewer strong connections within the food web. One of the most uncertain results is between juveniles and adults of the same species. This suggests that some predator/prey relationships (e.g. competitive links between WP and POP) seem more certain than the stock-recruitment relationship between juvenile and adult WP – the total overall production (i.e. food available to all planktivores) may be more certain than the relative age structure of each population. The implication for recruitment studies is that we should study a range of ecosystem effects over time. Counter to conventional wisdom, recruitment predictions and stock/recruitment relationships may be more uncertain than predictions based on predator/prey relationships. In terms of focus for future research, it suggests that some species (e.g. POP, SF) are less connected to the ecosystem, and the benefits of examining multispecies interactions for these two species may be low compared to WP, PC, and ATF. This highlights the importance of continuing to improve the skill of predictive dynamic models that assimilate the complexities of the broader ecosystem and their impact on the success of early life stages.

6. Application of model results to fisheries management

6.1 Use of recruitment estimates in stock assessments

Fisheries management often aims to maintain a population at or above the biomass that provides maximum sustainable yield (B_{MSY}). B_{MSY} is strongly influenced by the productivity of a stock, and target biomasses for stocks in the North Pacific including the GOA, are set using either estimated stock-recruitment relationships or a proxy for B_{MSY} (NPFMC, 2015). Confidence in recruitment estimates (rather, estimates of cohort strength when a cohort is first monitored by surveys) may be low depending on the age individuals recruit. Therefore, the management reference points (e.g. target biomass and yield) for most federally-managed groundfish in Alaska are not based on maximizing theoretical yield calculated from uncertain stock-recruitment relationships, but rather on a more precautionary adult-based spawner/recruit biomass proxies (NPFMC, 2015).

Recruitment estimates based on single-species stock assessments are model outputs, reflecting several tunable parameters based on simplified assumptions, such as the value of age and time-invariant natural mortality. The stock assessment models have been refined over time given their basis for determining stock status (e.g. whether it is overfished) and sustainable harvest levels. The uncertainty in stock assessment models has increased in recent years, especially following unanticipated ecosystem and environmental impacts. As such, the Alaska groundfish management system has adopted methods for reducing quotas using control rules and assessment outcomes based on quantification of ecosystem risk (Dorn and Zador, 2020). This “risk table” approach relies on indicators of ecosystem processes, both from direct observations and as derived from ecosystem models. One goal of IERPs is to further understand ecosystem processes to better predict population fluctuations that could be used to improve recruitment predictions, quantify ecosystem risks not captured in single-species assessments, inform fisheries management decisions, and forecast production. This is particularly relevant if model results could improve estimates for context-dependent shifts in key input parameters to stock assessment models (e.g. virgin recruitment, R_0; the natural mortality rate M; and steepness of the stock-recruitment relationship h; Punt et al., 2020).

Predicting recruitment (at age-0), as our IBM’s currently do, may not be indicative of stock projection. Still, there may be value to short-term forecasts for short-lived species, especially in terms of evaluating potential risks to upcoming recruitment. For example, an unanticipated marine heatwave occurred in the GOA between 2014-2016, leading to major declines in survival of juvenile and adult Pacific cod that were not detected until those cohorts matured in later years (Barbeaux et al., 2020). If models could provide recruitment estimates based on modeled oceanographic conditions before recruitment is observed in the surveys for adults, managers might develop control rules that use that information in advance. Additional information (e.g. recruitment indicators from IBMs such as those developed in the GOAIERP) may be useful in supplementing single-species stock assessments. Context and goals are important; a recruitment indicator from a model such as an IBM should *not* be expected to provide tactically precise estimation for maximizing yield. Rather, the predictions of an IBM (or most other ecosystem models) might more effectively focus on improving adaptability in management, by either anticipating or informing the response to events or by further accounting for environmental effects and ecosystem interactions when evaluating and implementing management action.

Management strategy evaluation (MSE) is a simulation framework that quantifies the expected performance of management processes, using summary statistics derived from operational objectives (Sainsbury et al., 2000). It attempts to model the entire management system, including the ‘true’ state of the resource, stock status, management advice, and decision processes, as well as fleet dynamics. MSEs can be used to assess assumptions (Smith, 1994; Smith et al., 1999) and consist of three components: an operating model, an estimation model, and a harvest control rule (HCR). Operating models simulate populations and can be based on stock assessments (Smith et al., 1999; Punt et al., 2016a), or indeed the ROMS physical system model, the NPZ lower trophic level model, and IBMs of focal fish species developed in the GOAIERP. Estimation models attempt to describe the dynamics of those populations based on generated observations. Various operating models might be used to evaluate the impact of incorrect assumptions about the population dynamics in the estimation model (e.g. Punt, 2003; Cur some non-essential text A’mar et al., 2010). Ecosystem models and IBMs might provide diagnostics to identify data gaps and/or conflicts. A critical component to this, and one that needs to be iteratively evaluated, is model skill (see section 7.3).

6.2 Use of dynamic ecosystem models

Dynamic ecosystem models, such as the physical oceanography model and the lower trophic level models used in the GOAIERP, can be useful to management in multiple ways. These Eulerian models can be used to provide an alternate way to estimate environmental conditions between surveys (in space and time) that is not based on interpolation of survey data. These conditions provide a more complete picture of the ecosystem, thus allowing a broader context for interpreting observations, for example through "risk tables". In addition, relationships between hindcast ocean conditions (validated against survey data) and fish production or stock status are being used as part of the National Oceanic and Atmospheric Administration's (NOAA) Rapid Climate Assessment (Spencer et al., 2019) to prioritize future research based on which species show the most sensitivity to measured variability as well as long-term forecast decisions. For example, nowcasts of ocean conditions from a ROMS model of the Bering Sea (Kearney et al., 2020) are currently included in the multispecies analysis of Bering Sea Walleye Pollock as part of that region's pollock stock assessment (Holsman et al., 2019). These modeled ocean conditions, if related theoretically to fish production, may be used as indicators during the management process to address uncertainty in measurements of the current ecosystem state. If current ocean conditions do not favor recruitment that might add strength to a stock assessment estimate of poor recruitment and support more precautionary measures until recruitment indices are later validated through the sampled abundance of adult fish.

In addition to providing direct, tactical management advice based on the modeling of past and current ocean conditions, the results of dynamic ecosystem models are important for strategic planning, especially in light of ongoing and future climate change. For example, the direct coupling of Bering Sea ROMS-NPZ outputs, projecting ocean conditions out to 2100, was used to drive a food web model of the Bering Sea ecosystem to assess the impact of alternative management strategies on the long-term sustainability of key fish stocks (Whitehouse et al., 2021), Such end-to-end coupled modeling efforts can test the long-term resilience of current fisheries management strategies (Holsman et al., 2020), and are an important component of planning management strategies in the face of climate change, for example through formal fisheries ecosystem plans (NPFMC, 2018).

Incorporation of ecosystem-level scientific advice into effective decision-making for marine resource management is increasingly being part of a larger synthetic process including stakeholders, scientists, decision-makers, and the public. Examples of such an approach are Integrated Ecosystem Assessments (IEAs), which aim to be "a synthesis and integration of information on relevant physical, chemical, ecological, and human processes in relation to specified management objectives" (Levin et al., 2009). A suite of models for an ecosystem, including ocean process models and a range of fisheries models, as described in Punt et al. (2016b) and including single-species, multispecies, and IBMs, can contribute strongly to providing strategic advice.

6.3 Application of IBMs

IBMs have been used for several purposes, including hypothesis generation and testing, defining marine protected areas and spawning areas, stock structure studies, and connectivity and recruitment studies. Among these, hypothesis generation and testing are probably the most powerful. The IBMs developed under the GOAIERP provide a holistic way of looking at how the early life stages of a groundfish species interact with the environment in a way that surveys and process studies cannot. They encapsulate our best understanding of species' early life history and, by providing a way to "scale-up" results from process studies and surveys to a much larger area, IBMs can help develop a mechanistic understanding of the processes underlying fisheries population trends.

Management of marine resources could also benefit from IBMs that quantify larval connectivity. This knowledge might help guide policy because fished stocks are frequently not constrained within the geopolitical boundaries in which they are managed. IBMs can reveal larval 'corridors' (i.e. spatial regions that regularly concentrate and nurture pelagic larvae during their ontogenetic migration to nearshore environments). Stressed fisheries may benefit from the establishment of a network of selectively-located marine protected areas corresponding to IBM-identified critical regions e.g. spawning or nursery areas. Our findings, for example, indicate that there is likely at least some connectivity between the pollock stocks in the GOA and the Bering Sea (Parada et al., 2016) and between sablefish in Canadian waters south of the GOA, and the GOA population (Gibson et al., 2019). These findings could be potentially transformational for the management of these stocks and warrant further investigation.

7. Model development within an Integrated Ecosystem Research Program

7.1 Model development and design – approach and constraints to integration

The development and application of numerical models to explore ecosystem dynamics in the context of an IERP provides an opportunity to enhance overall program goals, focus research questions, and provide a broader context for the interpretation of observational data and process studies. The IERP framework is designed such that integration of the various research efforts is a fundamental program goal. In this context, modeling could serve as a way to approach this integration in a synthetic, comprehensive, and quantifiable fashion. Due to prohibitive costs, field or laboratory studies directly address only specific, tightly-focused hypotheses regarding environmental processes over generally limited temporal, spatial, and environmental extents. In addition to directly addressing the project hypothesis, models within the GOAIERP aimed to provide a broader spatial and temporal reference framework to aid in the interpretation of observations and to identify areas of sampling. In this context, model results can guide sampling design or follow-up field or lab studies by suggesting times of year or regions of interest, critical to better resolving life history and population processes, potentially leading to reduced uncertainty. Numerical models can also provide a means to synthesize field observations and lab studies using an objective, coherent framework to integrate data across larger spatial and temporal scales to predict regional-scale consequences.

7.2 Timing

Within an integrated research program, time needs to be allotted to allow incorporation of the results of field and lab studies within the models (e.g. new parameterizations of model processes or initial conditions). Fundamental questions related to timing and modeling in the context of an integrated program are (1) sequencing, and (2) the purpose of the modeling effort. Most new data from the GOAIERP project became available only at the end of the project. Within an IERP, modeling, fieldwork, and lab studies should thus be approached as a set of interactive, iterative components, and time and opportunities for interaction among these components needs to be factored into program design to achieve true integration. Models might be used at the outset to identify questions and processes for the field study provided time and effort had been previously dedicated to model development and implementation – either under a prior program or under the first phase of an IERP. Alternatively, sampling and field analyses might be conducted in advance to aid in model conceptualization and inform model development and parameterization, or validation. This issue of timing presents one of the greatest challenges in an IERP and requires careful consideration. The appropriate timing of model development will depend on how the modeling objectives are defined within the context of the overall study. If models are intended to guide sampling, they need to be able to produce the required outputs early in the program, prior to survey design. Within the GOAIERP, the coupled ROMS-NPZ model had been developed in advance of the implementation of a field program and the modeling team was able to provide the broader GOAIERP research community with output from multi-year, physical, and lower trophic level simulations at the program onset. This early availability of model output was used to guide the sample design of the observational program (Dickson and Baker, 2016). For example, the initial sampling design proposed was focused on two grids on the eastern and western sides of the GOA. Model outputs indicated that the large spatial gap in the central GOA was problematic due to the along-shelf connectedness of currents in the GOA and the original sampling design was modified accordingly.

Timing within the program duration is also an important consideration. The GOAIERP was conducted over a relatively short, four-year time-frame. This and the inherent delay in the availability of the observational data meant that there was only a limited amount of time for conducting multiple iterations and improvements to any of the models. Only at the end of the GOAIERP were we able to utilize the results from the observational components to improve the representations of physical and ecological processes in the numerical models.

7.3 Model validation

7.3.1 ROMS and NPZ model validation

Validation of the lower trophic level and physical models used to drive the IBMs is possible to at least some degree using bio-physical observations from shipboard sampling, moorings, and satellite observations (Coyle et al., 2012, 2013, 2019; Hinckley et al., 2009b; Hermann et al., 2009b), However, the mesoscale features of the GOA are influenced by fine-scale details of atmospheric forcing (e.g. storms, episodic events) and chaotic (nonlinear) physical processes; consequently predictions from the hydrographic and thus the lower trophic level models will never precisely match field observations at any given location and time. Thus, point-by-point comparisons of model and data can be misleading, especially when the data used for model validation do not come with associated measures of error, and may lead to disregarding informative results. Ideally, the models will capture summary statistics (e.g. the total kinetic energy) of eddies and meanders in a given year, even if they cannot precisely capture the detailed timing or locations (Coyle et al., 2012). Numerical models can only be as "good" as the field and lab studies that support them and the utility of model-data comparisons is complicated by the varying spatial and temporal resolution of the observations. Because of limits to data availability, we were only able to assess the skill of the Eulerian hydrographic and lower trophic level models by comparison of seasonal climatologies from aggregated data and model output (Hermann et al., 2019; Coyle et al., 2019). Confidence in a model to replicate ecosystem dynamics on this broad time scale should give confidence in its ability to suggest mechanisms and processes important to ecosystem dynamics.

7.3.1 IBM validation

IBMs built on top of the lower trophic level and physical model add another layer of assumptions and potential compounded errors. There are limited methods that can be used to validate IBM predictions of larval dispersal and transport of individuals (North et al., 2009). Comparing trajectories from model predictions to those from satellite-tracked drifters is of minimal use due to the limited number of drifters that can be deployed, and the predisposition of drifters to diverge from larval fish trajectories because of larval behavior. Chemical marking of individuals might be a useful validation technique but is only applicable when populations are small, mortality is low, and the likelihood of recapture is reasonable. One of the most straightforward ways to corroborate dispersal and transport simulated by an IBM is by comparing modeled and empirical spatial distributions of larvae and juveniles. Although it cannot be known if individuals from spawning sites are the same individuals that are caught during later surveys, this comparative approach can be useful when the sources of individuals caught in the field are relatively well known. Differences in spatial distributions between IBM model output and survey data may be attributed to several factors including differences in initial conditions (i.e. the location and timing of modeled and actual spawning). Limitations in the hydrodynamic model, as well as limitations in simulating larval and juvenile behaviors (i.e. the absence of directed swimming) could also result in a miss-match between IBM output and survey data.

Even if IBMs might be evaluated based on their ability to match observations, there is an enormous data deficit for model validation that cannot realistically be addressed, because of the necessary spatial (i.e. high resolution, large extent) and temporal (i.e. high resolution, long term) sampling required to resolve potentially-confounding effects. A better approach would be to compare (appropriately averaged) model results under different scenarios of assumed critical processes to generate testable hypotheses that can be subsequently addressed by targeted fieldwork. In an IERP, part of the goal of the observational data collection should be to improve the models' characterization of potentially-critical processes – by design, not just happenstance. Such an approach would help ensure that the data collected are useful to the modeling effort and, in turn, the model results are reflective of reality. Full consideration of the data required to support model development and validation during the design phase of the field program would facilitate better integration.

Model validation and model improvement should be treated as an iterative process where mismatches between model and data can be used to improve the model and the surveys (if they can be specifically designed to compare with model output). We recommend a multistep process for the validation of spatial output of biophysical IBMs, starting with visual comparisons and simple descriptive statistics, followed by the calculation of indices for features of interest, and finally, using statistical and geostatistical approaches that can give measures of statistical significance to the differences/similarity between spatial model output and data. For some purposes, i.e. management applications, "success" in validation may need to be pre-defined by delineating success thresholds. In addition to broad comparisons of GOAIERP IBM model output to presence-absence data, the principal datasets available to compare with predictions were the recruitment time series for each species, estimated as part of stock assessments conducted by NOAA Fisheries (Spies et al., 2015).

7.4 Interaction

Determining the impact of advection and the environmental experiences of early life-stage groundfishes as they are transported between spawning and nursery areas is an inherently interdisciplinary problem that requires consideration of the physical and lower trophic level environments in conjunction with early life history dynamics. Interaction and integration between program components are essential. Here there are clear challenges. The GOAIERP involved over 50 researchers from a wide background of disciplines. Although the central hypothesis for GOAIERP was established prior to solicitation of individual research projects, the specific observational and modeling efforts in this program were proposed in isolation. As such, despite the initial conceptualization of how the field data could guide modeling efforts, the models were largely divorced from the field and lab studies conducted as part of the GOAIERP. We found that, while many of the researchers were open to the idea that models could be a useful tool in survey design and data interpretation, initially there was an underlying reluctance to fully embrace modeling tools as useful additions to the program. This skepticism was partly due to mistrust in the ability of models to adequately represent ecosystem and life history dynamics, and partly to unfamiliarity with the proposed modeling approaches. More effort might be devoted to demonstrating the utility of models, not only to explain mechanistic processes but also to suggest further research topics and sampling design.

While the level of *interaction* between the modeling and field/lab components improved substantially throughout the four-year GOIERP, there was a consensus that there was insufficient time in the program allotted to promote effective *integration* between the modeling, field, and lab components. In addition to the challenges of matching the timing of field programs and model development, lack of ‘trust’ in the models may hinder full integration between modelers and observationalists. As such, opportunities allowing (or forcing) team members from different IERP components to come together, interact, and understand each other’s needs and contributions was time well spent. Within the GOAIERP, directed program management and successive annual meetings provided improved opportunities for such interactions: integrated presentations that necessitated cross-disciplinary interaction prior to the meetings, required ‘speed dates’ between small groups of researchers that may have never previously interacted, and time for general discussion. In retrospect, we feel that the importance of this “face” time cannot be overestimated.

8. Successes and lessons learned

8.1 Successes and shortfalls of the IBM modeling effort

Here we discuss the general advances and limitations experienced in the GOAIERP modeling effort related to model development and validation, developing a conceptual framework, and synthesizing insights related to environmental indices and IBM outputs related to connectivity, trajectory, and path analyses. Insights into each species and IBM framework and what we have learned about potential recruitment mechanisms are summarized in Table 3.

8.1.1. IBM methodological development

One of the principal successes of the modeling effort was the methodological advancement in IBMs. By providing a common objective and highly coordinated iterative process for exchange between modelers approaching a common question, in a common system, with similar tools but distinct targets (i.e. unique species and data resolution), the GOAIERP enabled a useful exchange of ideas and approaches. By leveraging existing development code and analysis tools GOAIERP was able to quickly produce five new or significantly updated, regionally-specific, models.

8.1.2. Insights from connectivity analyses

Overall, model simulations showed agreement with our previous knowledge of prospective viable spawning areas (Fig. 13). The exact spawning areas for PC, POP, SF, and ATF are not known. IBM results for both POP, ATF, and SF indicate that spawning areas in the eastern GOA would generally be more successful in terms of recruitment to inshore nursery areas than those in the western GOA, due in large part to the counter-clockwise nature of the general GOA circulation pattern and the offshore spawning areas of these species. Typical dispersion distances on the order of several hundred km were found for these species. For PC, the IBM results suggest settlement from all spawning areas is high, except for the West Shumagins area as individuals spawned there were most likely to be swept offshore into the GOA basin. These results point to the immediate need to refine our knowledge of actual spawning areas for PC, POP, SF, and ATF. More is known about WP spawning locations, and the prevailing hypothesis is that Shelikof Strait is the primary pollock spawning area in the GOA while the Shumagin Islands provide the main nursery area. The WP IBM suggests that the spawning areas in the GOA most likely to produce successful settlers are indeed in Shelikof Strait.

Below we summarize what the GOAIERP IBMs tell us about likely connectivity between spawning and nursery areas for each of the five groundfish species. While connectivity appears to be able to explain a portion of recruitment variability, it is clear from our analysis that it is not the only factor.

- *Walleye Pollock:* The WP IBM suggests a pattern in connection strength characterized by higher retention along the Inner Shelf domain (40-90%) and lower retention in the inner offshore region at the larval stage (30-40%). Connectivity between spawning grounds in the inner shelf domain (Kenai, North Kodiak, South Kodiak, Chirikof, East Shumagin, West Shumagin) and nursery grounds downstream (to the southeast) had a probability of ~0.2. A weaker connection (at the larval stage) with similar probability values was also demonstrated between spawning areas in the inner shelf domain and the inner offshore domain. The strongest connection (probability ~0.1 to 0.4) was between the inner offshore domain and the inner shelf domain and is evidence for cross-shelf transport to the inner shelf. For juveniles, a direct relationship was found between assessment-based recruitment anomalies and the PC1 from the EOF analysis (r=0.41, p=0.11), highlighting the importance of the environment through which the individuals were transported.
- *Pacific Cod*: The PC IBM indicates that the young stages of PC generally do not disperse far from natal areas. Retention of individuals in areas where they are spawned was the strongest connectivity pattern followed by cross-shelf transport from the deep spawning areas to nearby shallow nursery areas. The restricted transport that we observe in our model results is, in part, because PC eggs are attached to the bottom for nearly a month of their early life and because the movement of simulated juveniles is restricted upon settlement. Settlement strength in Icy Bay and the West Shumagin area had the strongest correlations with recruitment estimates from stock assessments for PC. We found significant correlations between large-scale climate indices (i.e. the NPI and the MEI) and hypothesized that slower gyre circulation enhances retention and cross-shelf transport to nearshore nursery areas.
- *Pacific Ocean Perch*: The POP IBM indicates that dispersal distances for individuals successfully settling were on the order of several hundred km. Connectivity is strongest (median~5%) between parturition areas in the southeast (Sitka and Cross Sound) and nursery areas in the central GOA, while somewhat weaker connections (median~3.8%) exist between Cross Sound and nursery areas in Icy Bay. The fraction of individuals originating from the Sitka and Prince William Sound spawning zones that successfully settled in any nursery area explained the greatest fraction of variance (66%) in assessment-based recruitment estimates (adjusted r^2=0.62; empirically-determined family-wise p-value <0.05).
- *Sablefish:* The SF IBM suggests that the strongest connectivity (median~1.0%) in the GOA is between spawning areas over the continental shelf in the southeast (Sitka and Cross Sound) to shallow nursery areas in the central GOA. The direction of connection was generally from east to west, with very little retention of individuals within the same alongshore zones, or connectivity to regions to the east of a spawning zone. The total connectivity (i.e. the proportion of individuals settling to suitable nursery sites anywhere in the GOA, regardless of spawning area) correlated more strongly (r=0.45, p= 0.08) with assessment-based recruitment estimates than the connectivity associated with any one spawning area or settlement site.
- *Arrowtooth Flounder*: Similar to the results for both POP and SF, the ATF IBM suggests connectivity (median~3.5%) is the strongest between spawning in Sitka and Cross Sound and coastal nursery areas in the central GOA. However, in contrast to the results for those species, the second strongest connectivity (median~2.5%) was between

spawning areas in Yakutat and Icy Bay and nursery areas in North Kodiak. The fraction of individuals successfully settling in nursery areas in North Kodiak, regardless of spawning area, was positively correlated (ρ=0.64, but the p-value, corrected for multiple comparisons, was not significant) with estimates of recruitment from stock assessments and accounted for 34% of the variance in recruitment.

8.1.3 Insights from trajectory and path analyses

Environmental conditions experienced by the early life stages of the five focal groundfish species may be equally as important in determining recruitment success as connectivity. For example, in the case of SF, lower trophic level production during the first year of life, as individuals are transported from the deep offshore spawning areas to the shallow coastal nursery areas, correlated as strongly with recruitment as the connectivity index. Together these two variables were able to account for 50% of the recruitment variability as predicted by the stock assessments.

8.2 Using ecosystem modeling approaches to inform fisheries management

Depending on age at recruitment, confidence in the most recent year's predictions may not be strong. As a result, management strategies in Alaska currently use adult-based spawning biomass proxies (NPFMC, 2015). There have been increasing calls for EBFM (Link, 2002; Pikitch et al., 2004; Link, 2010; Fogarty, 2014; Fulton et al., 2014; NMFS, 2016) as it is clear that reductionist single-species stock assessment approaches that ignore broader environmental conditions overlook important implications and impacts on recruitment and survival (Hollowed et al., 2001; Duffy-Anderson et al., 2005). Model-informed estimates of the success of early stages and recruitment of juvenile fish into the adult population in the context of climate-driven variability could promote a broader ecosystem understanding and improved predictions of year-class strength for these GOA fish populations.

8.2.1 Use and application of existing data and models to predict recruitment

GOAIERP models might be applied to inform recruitment estimates in the following ways:

- ☐ ROMS-NPZ outputs might be applied to understand patterns in annual recruitment using retrospective data and be used to develop new data streams to improve predictive capacity and determine environmental conditions that increase recruitment success or failure.
- ☐ IBMs for each of the focal groundfish species might be updated with emerging species-specific information and used to further identify data gaps and guide the development of process studies.
- ☐ IBM, ROMS, and NPZ models might be used to better inform differences in the distribution of recruitment across distinct spatial domains.
- ☐ Data and model outputs might be applied to characterize important ecosystem processes at distinct local and regional scales within the GOA.

8.2.2. Development of a conceptual framework and species profiles

One success of the modeling effort has been to refine conceptual models and profiles for each of our focal groundfish species. This effort has allowed us to identify emergent properties of groundfish populations, distinguish significant phenomena determining the response of populations and communities to perturbation, and consider what aspects of biological or behavioral traits promote resilience species level (e.g. life history variation, phenotypic plasticity), community level (e.g. functional redundancy), ecosystem level (e.g. network connectivity). This information might help direct climate vulnerability analyses to assess the current status and future risk to populations, and also in determining which stocks would benefit from further integration of environmental data in their assessment.

8.2.3. Development of predictive environmental indices

We had hoped the conclusion of our modeling work would enable us to develop a series of indices, or identify easily measurable variables that would be useful for predicting recruitment of the focal groundfish species. Our results suggest that recruitment variability is more complicated to predict. While the variability in successful transport of individuals from spawning areas to nursery grounds can explain some of the variability in recruitment, the variability in transport could not be tied to just one or two atmospheric or oceanic variables that could be easily measured. We had only a relatively short time series of model outputs to use in our multiple regression analyses so our statistical power was limited. With longer time-series it might be possible to identify more powerful indices or combinations of indices. Despite our inability to identify simple recruitment prediction indices, our work has helped shed light on the mechanisms that may underlie successful recruitment. For example, in the case of PC, slower gyre circulation may lead to increased retention and reduced transport, which may enhance recruitment. For species that spawn along the continental shelf break (POP, SF, ATF), conditions that promote on-shelf transport in the east and higher spring and summer production may favor increased recruitment.

8.2.4. Ecosystem approaches to management

The IEA process (Fig. 14) is a iterative approach to EBM or EBFM and involves several steps that integrate science and management. Ecosystem-based management goals should be established with strong engagement from managers, stakeholders, and the public. Ecosystem indicators must then be developed to track progress towards goals and ecosystem assessments conducted to determine ecosystem status, risk, and uncertainty. Ecosystem models, and species-specific models embedded in larger ecosystem models such as those presented here, can help to 1) identify policy tradeoffs inherent in goal setting (e.g. tradeoffs between predators and prey, or habitat and fishing); 2) identify or produce indicators (e.g. nowcast ocean conditions); 3) describe the theoretical or empirical relationship between indicators and goals (e.g. how productivity is linked to ocean conditions); 4) estimate ecosystem-based reference points during stock assessments (e.g. species vital rates, or multispecies sustainable yields); 5) quantify uncertainty and identify where established ecosystem relationships or management policies may no longer hold (e.g. ecosystem tipping points, thresholds or regime shifts); 6) fill in observation gaps, predict future conditions; and/or 7) serve as simulation testbeds for management strategies. Uses may be found for individual model outputs derived in the analyses described here to inform the effects of climate and oceanographic conditions on species outcomes and interactions.

8.2.5. Ecosystem indicators report card

As part of its annual stock assessment cycle, the National Oceanic and Atmospheric Administration (NOAA) Alaska Fishery Science Center (AFSC) produces Ecosystem Report Cards and Ecosystem Assessments for the Bering Sea, GOA, Aleutian Islands, and Alaskan Arctic (e.g. Zador et al., 2017b). These report cards contain a subset of relevant indicators chosen by ecosystem experts in consultation with stakeholders. Indicators are chosen to track ecosystem status from climate through living resources and ultimately humans. This information is presented to the North Pacific Fisheries Management Council immediately prior to quota-setting and has been used to support the adjustment of fishing quotas downward in cases where extra precaution was warranted (Dorn and Zador, 2020). Ideal indicators fill gaps in knowledge, can be characterized on annual scales, have long time-series, and are available “now” (Stephani Zador, NOAA-AFSC, personal communication). AFSC ecosystem assessment authors are working with PIs of the GOAIERP project to transition GOAIERP research into new indicators that might be produced on an ongoing basis.

9. Conclusions

The GOA is a dynamic and highly productive ecosystem that supports important fisheries and the communities dependent on them (Ormseth et al., 2019). The GOAIERP was one among many efforts made to develop large, coordinated, integrated research programs to improve understanding of ecosystem dynamics and fisheries population fluctuations in the North Pacific (Lindeberg et al., 2022). Several important findings from this effort have emerged.

9.1 The gauntlet hypotheses

The GOAIERP proposed the 'gauntlet hypothesis' – that the primary determinant of year-class strength for GOA groundfishes is early life survival. It was proposed that this is regulated in space and time by climate-driven variability, offshore and nearshore habitat quality, larval and juvenile transport, and settlement to suitable demersal habitat. We found that while the connectivity between spawning areas and nursery sites alone was able to explain significant amounts of variability in recruitment of some groundfish (i.e. SF ~20%, POP ~30%, ATF ~30%) it did not explain more than half of the recruitment variability for any species. While some transport dynamics may have been missed or underestimated, due to the resolution of the model and its skill in simulating fine-scale oceanographic and biological processes, our findings lead us to reject modeling hypothesis H1 and conclude that the proportion of young fish transported from offshore spawning areas to nearshore nursery areas cannot be the driving factor affecting recruitment. This points to the importance of environmental influences other than transport on young larvae (e.g. spatial predation) or to post-settlement processes in determining recruitment success. Because we could not generally incorporate mortality into the model, H2 remains largely unanswered.

Our modeling studies suggest that the eastern and western GOA are substantially different with respect to their contribution to important spawning and nursery area habitat. For the species that spawn on the shelf break (i.e. POP, SF, ATF), the eastern GOA appears to be much more likely to have spawning grounds that would produce successful recruits to populations in the GOA. Spawning areas for these species in the western GOA appear more likely to be providing recruits to populations (if any) downstream, perhaps to the southern side of the Aleutians or into the Bering Sea. Thus, it appears that the dominant east-west physical transport is key to driving these differences, and probably far more important than any biological differences in the food web in either region for these species. Conversely, the western GOA appears to be more important for WP and PC due to retention mechanisms. For PC, many fish that are spawned in the eastern GOA, especially those that spawn in deeper waters, were transported out of the GOA before being able to settle so were not recruited into the GOA population. For WP, historically the largest spawning concentrations occur in Shelikof Strait in the western GOA. However, secondary non-Shelikof aggregations in the western GOA have increased over time — potentially due to altered homing habits in response to changing environmental conditions (Ciannelli et al., 2007). Simulations have suggested the connectivity of GOA spawning regions to the Bering Sea through transport via Unimak Pass. However, the contribution of GOA spawning to Bering Sea recruitment is not yet understood.

9.2 Integrated research

The process of integration was challenging, but the GOAIERP program was intentionally designed to promote the integration of findings to better interpret results and enhance understanding of ecosystem dynamics. Following this experience of incorporating modeling into an IERP we present the following key factors that should be considered to maximize success when incorporating modeling into an IERP or other multidisciplinary research program:

- ☐ Carefully consider the development status of the proposed models, including that additional development/tuning/validation time, will be needed within the IERP.
- ☐ Ensure the data needed for model development will be collected by the field program.
- ☐ Consider the time frame of the sampling program in relation to the model development to ensure the data are available in sufficient time for incorporation into the models.
- ☐ Schedule regular, guided meetings between model team members and field program participants to ensure maximum integration of these IERP components.
- ☐ Pre-determine how the ‘success’ of the models is to be judged.

Overall, the completion of the GOAIERP modeling should be seen in a management context as the start of a process (e.g. an IEA), rather than a single “delivery of results”. Within management agencies such as NOAA, resources are being increasingly directed towards the operationalization of ecosystem-level models; working with these agencies, the GOAIERP modeling legacy may improve EBFM in the region. Following this experience, we highlight the following key factors for bringing models developed within the framework of an IERP into the management arena.

- ☐ Close coordination with the local management agencies before and during the IERP. Determine who the ultimate end users will be and how model output and insights could be incorporated into the existing management strategy.
- ☐ Determination of key ecosystem drivers, and understanding of the models’ abilities to capture variability in these drivers on short (annual) and longer (interannual->multi decadal) time scales.
- ☐ Successful incorporation of models into tactical and strategic decision-making requires support to keep the models maintained and updated.

More broadly, the development and application of numerical models to explore ecosystem dynamics in the context of an IERP can enhance overall program goals, focus research questions, and provide a broader context for the interpretation of observational data and process studies. Integrative numerical models can provide extrapolation to regional-scale implications for observed fine-scale processes. In turn, model results and sensitivity analyses can suggest biologically productive geographical areas or scientifically productive areas of inquiry, as well as sampling designs, for follow-up field or lab studies. Modeling, fieldwork, and lab studies thus need to be viewed as a set of interactive, iterative components within an IERP framework. Additionally, the IERP framework needs to provide the opportunity for interaction and the time for iteration among these components to achieve true integration.

9.3 Informing management

An ongoing challenge to model development in the context of fishery management is to determine how to direct models and how to interpret results to better understand, hindcast, and predict stock status and trends. One challenge is determining the appropriate processes to consider and the assumptions involved. Another is distinguishing cause and effect versus correlation. Some of the most useful products from this effort may include the formal development of detailed species profiles, including information on early life history, known ecological trends, and hypothetical mechanisms related to transport and survival. These profiles should be maintained and updated with new information, as available. They might also inform future sampling efforts and survey designs (e.g. trawls, acoustics, larval sampling) as well as laboratory analyses (e.g. diet and energetics). IBMs have been successful in determining important habitats relevant to spawning and settlements. Results also identify key questions to explore further related to climatological effects, stock connectivity, and the potential for stock production and export beyond ecosystem boundaries (e.g. advection of GOA produced larvae to the Aleutian Islands and the eastern Bering Sea). Overall, the models provided insight to understand recruitment processes, important legacy products and will contribute to future GOA ecosystem studies.

9.4 The art of modeling

The GOAIERP modeling effort was useful, not only in informing understanding of recruitment in groundfish, and in integrating models into the program, but also as an exercise in model development. In any modeling approach, it is essential to determine not only what to include, but what not to include. Feasibility, simplicity, and parsimony are all important considerations. Several aspects will influence these decisions, including what data are available, what data are appropriate or accessible to the models, and the relative perceived importance of those data to model outputs. In this context, the elements critical to determining recruitment seem to include transport, prey fields, predation, and habitat. Fish are not passive particles and while the GOAIERP IBMs included stage-specific growth and vertical movement capabilities, future work might consider how the outputs presented would be influenced by additional behaviors, including more complex directed swimming (i.e. towards prey or geographical regions) and more complete bioenergetics for growth and natural mortality. Local-scale physical features (e.g. the extent to which canyons channel larvae and contrast with along-shelf flow) and episodic events (e.g. gap winds and associated increased cross-shelf flow facilitate cross-shelf transport) are also important to transport and deserve further examination. It would be worth considering how a physical model with finer spatial and temporal resolution (i.e. refined vertical water column complexity, temporally-resolved tidal currents and tidal stream transport, flow through canyons, and bottom currents) would influence IBM predictions. Finally, it is important to consider, on a theoretical level, how to best use snapshot-type data (e.g. oceanographic data at a single location and time) to inform, validate, and model ongoing dynamic physical processes.

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Tables

Table 1. Summary of IBM details for each of the five focal species. Potential life stages include eggs (E), yolk-sac-larvae (YSL), feeding larvae (FL), small and large prefexon feeding larvae (prF_{SM}, prF_{LG}), postfexon feeding larvae (poF), Epipelagic juveniles (EPJ), juvenile settlement stage (J_{set}), juvenile benthic stage (J_{ben}).

Species Trait	**Pollock**	**Cod**	**ATF**	**POP**	**Sablefish**
Life Stages	4:E, YSL, FL, J	6:E,YSL, prF, poF, EPJ, J_{ben}	8: E, YSL_{sm},YSL_{lg}, pre-FL_{sm}, pre-FL_{lg} post-FL, J_{set}, J_{ben}	5: FL_{pre} , FL_{post}, PJ, J_{set}, J_{ben}	5: E, YS, FL, EPJ, J_{set}
Attaches to bottom	No	Yes, E & J_{ben}	No	No	No
Stage-specific growth	Yes	Yes	Yes	Yes	YEs
Temperature-dependent growth	Yes-E, FL, stages	Yes-all	No	No	No
Stage-specific depth preference	Yes	Yes	Yes	Yes	Yes
Terminal velocity/vertical position	E, YSL	E, YSL	E, YSL	E, YSL	E, YSL
Diel Migration	FL,J	Yes- FL_{post} & EPJ	No	No	only J_{set}
Vertical directed swimming	Yes-J	Yes- YS, pre-FL_{pre} , FL_{post}, EPJ,	Yes	Yes	Yes
Horizontal directed swimming	Yes-J	No	No	No	No
Consumption	Yes-FL,J Based on historical data of prey density	No	No	No	No
Predation	Yes- on juveniles, based on ground fish predation data	No	No	No	No
Competition	No	No	No	No	No
Unresolved Processes	Juveniles directed swimming. variability in mortality – i.e. temporally-and spatially-explicit groundfish predation. Submesoescale processes	Potential juvenile movement. Consumption Mortality	Directional swimming towards preferred habitat; mortality consumption, mortality, temperature-dependent growth	Directional swimming with degree of natal homing in some life stage; mortality consumption, temperature-dependent growth, mortality	Directional swimming towards preferred habitat type consumption, mortality, temperature-dependent growth Transport mechanism to known and consistent nursery sites i.e. St. John Baptist Bay

Table 2. Summary of research questions and the approach taken/proposed to answer the questions, and which of the two hypotheses this helped address.

Research Question	**Method**	**Hypothesis**
Were the successful settlers concentrated into a narrow alongshore zone?	Connectivity analysis	H1
Where did the successful settlers come from?	Connectivity analysis	H1
Can connectivity between individual spawning and recruitment sites predict overall recruitment strength?	Connectivity analysis	H1
What were the paths followed by young fish that were spawned in different regions?	Trajectory analysis	H2
What were the differences in paths followed by the successful settlers by those that never settled, or by those that exited the GOA?	Trajectory analysis Path analysis	H2
What were the physical processes (e.g. eddies, currents) that took young fish towards or away from favored nursery areas?	Trajectory analysis	H2
What were the topographic features that steered them towards or away from these nursery sites?	Trajectory analysis	H2
What were the temperature histories of successful settlers vs. non-settlers?	Trajectory analysis	H2
Was there an optimum duration of the pelagic stage for successful settlers?	Trajectory analysis	H2
How direct or indirect were these trajectories?	Tortuosity analysis	H2
What was the prey field experienced by successful settlers vs. non-settlers?	Trajectory analysis	H2

Table 3. Summary of mechanisms important to groundfish recruitment, as identified by the IBMs. Notable relationships (r or r^2) between model indices and estimates of recruitment from stock assessments are also identified.

Connectivity Analyses

IBM	Mechanisms Identified	Significant Correlations
WP	Connectivity showed that reaching the Shumagin West region as juveniles is more beneficial than having an early arrival as larvae to that nursery area, which is consistent with findings arising from examination of the tortuosity index	A positive correlation between recruitment anomalies and PC1 for larvae (r=0.41, p=0.11) An inverse relationship was found between recruitment anomalies and PC2 for larvae (r=-0.58, p=0.02)
PC	High larval retention in the Cook Inlet and along the Inner Shelf domain; the importance of Shumagin Islands as a nursery area	Settlement in Shumagin Islands vs MEI (r=-0.54, p<0.05), and vs. NPI (r=0.53, p<0.05)
POP	Connectivity was directed in a counterclockwise fashion, with typical dispersal distances ~100's km. More than 70% of individuals did not settle successfully. Individuals spawned in eastern GOA were much more likely to settle successfully. The probability of retention in the spawning zone was low.	Cross Sound to Prince William Sound (PWS) most strongly connected S-N pair (r^2=0.62, p<0.05)
SF	Sablefish settling in nursery areas in the GOA were most likely spawned in the eastern Gulf.	Settlement depth was the most influential parameter in determining Total Connectivity (r^2=0.72, p<0.05)
ATF	Similar to POP. More than 80% of individuals did not settle successfully.	

Trajectory Analyses

IBM	Mechanisms Identified	Significant Correlations
WP	Efficient and direct trajectories bring a larger proportion of WP to nursery grounds	The tortuosity index generated using the pollock IBM output showed an inverse relationship between the index and the stock assessment recruitment (r=-0.42, p=0.11).
	Submesoscale eddies might play a role in concentrating or reducing dispersion offshore affecting the direct arrival to potential nursery areas.	The number of anticyclonic and cyclonic submesoscale eddies are four times larger on the shelf than off-shelf in the western GOA, which is characterized by mesoscale eddies dispersing particles offshore
	Climate indices correlated with stock assessment recruitment anomalies and WP biophysical indices (Principal components of connectivity)	MEI was inversely correlated with stock assessment recruitment anomalies (r=-0.39, p=0.13).

		PC1 larval connectivity positively correlates to PDO ($r=0.53$, $p<0.05$).and AO ($r=0.46$, $p=0.07$), while PC1 juvenile connectivity is directly correlates to PDO ($r=0.41$, $p=0.12$).
PC	Short mean trajectories for successful settlers. Settlers concentrated nearshore Unsuccessful settlers in PWS (too deep) Many PC exit the GOA to the southwest	
POP	Considerable transport off the shelf; Potential for export from the GOA to the AI and/or the EBS for individuals spawned in the western GOA.	Nursery areas most frequently reached by those successful individuals were in the central GOA
SF	Early on-shelf transport in the eastern GOA.	Southerly wind in eastern GOA (Jan-March) $r=0.5\text{-}0.7$, $p<0.05$
ATF	Considerable transport off the shelf; potential for export from GOA to AI and/or EBS for individuals spawned in western GOA.	Most effective nursery areas were in the central and western GOA
Predicting Recruitment		
IBM	Mechanisms Identified	Significant Correlations
WP	Pollock recruitment appears to be positively affected by physical conditions that result in efficient transport to the nursery areas.	Inverse relationship between the tortuosity index and the stock assessment recruitment ($r=-0.42$, $p=0.11$).
PC	Lower temperatures and curved paths improve recruitment.	Degree days ($r=-0.58$, $p<0.05$) Tortuosity index ($r=0.55$, $p<0.05$)
POP		Annual total fraction of successful individuals from natal zones 2 Sitka and 6 PWS ($r^2=0.62$, $p<0.05$)
SF	-Cross shelf transport -Primary production -Strength of S-SE wind. Total connectivity between all spawning sites and nursery areas had a stronger correlation with recruitment than the strength of connections to or from a specific region.	Total Connectivity $r^2=0.2$, $p=0.08$ Total Connectivity + Annual cross shelf flow + Primary Production $r^2=0.59$, $p=0.01$
ATF	No significant relationships identified between connectivity indices and recruitment estimates.	None

Figure Captions

Fig. 1. Key features and location in the Gulf of Alaska study area. For orientation, the location of the detailed overview within the Gulf of Alaska is outlined (black box) in the top right inset. The full extent of the model domain (white box) is shown in the top left inset.

Fig. 2. The GOAIERP was a vertically-integrated hierarchical study of the physics, fisheries, and ecosystem of the GOA, partitioned among: the upper trophic level (UTL), the middle trophic level (MTL), the lower trophic level and physics (LTL), and modeling. Schematic illustrates the coupling of output from various models, coordination between process studies and modeling, choice and criteria for evaluating model outputs, interaction with human-induced impacts, and linkages between the scientific question and management needs. H1 and H2 refer to the two modeling hypotheses. The thick blue arrows indicate the flow of model output/input between the models used in the GOAIERP. The thin black arrows indicate the flow of information/data from the LTL, MTL, and UTL components into the models. The thicker black arrows indicate where model output informed H1 (dash) and H2 (solid).

Fig. 3. Conceptual models for IBMs of select Gulf of Alaska groundfish a) Walleye Pollock (WP), b) Pacific Cod (PC), c) Pacific Ocean Perch (POP), d) Sablefish (SF*),* and e) Arrowtooth Flounder (ATF). Life stages included in each IBM vary but generally include: egg, yolk sac larva, small feeding (SFPr) pre-flexion larva, large feeding pre-flexion (LFPr) larva, postflexion larva, pelagic juvenile, settlement-stage juvenile, and benthic juvenile (see: Gibson et al., 2019; Hinckley et al., 2019; Stockhausen et al., 2019a, 2019b. Larval drawings based on Matarese et al., 1989; illustrations by Beverly M. Vinter).

Fig. 4. Schematic illustrating the structure and direction of material flow in the GOA nutrient phytoplankton zooplankton model embedded in the ROMS physical oceanography model. Arrows indicate the direction of material flow.

Fig. 5. Connectivity matrices illustrate the annual median probability that individuals spawned as eggs in each alongshore zone (1-12) in the model domain (a) successfully settled in each alongshore nursery area for b) SF, c) ATF, and d) PC. Medians were computed across the 16-year simulation (1996-2011). For simplicity, the connectivity matrix shown for PC is for individuals spawned and settled within the < 70 m depth zone. PC individuals were also released and settled within additional depth zones, but the overall pattern of connectivity was similar. The connectivity to the GOA basin and areas outside of the model grid are not shown.

Fig. 6. Trajectories of Walleye Pollock spawned in Cook Inlet (ai), Kodiak Island (aii), and Shelikof Strait (aiii) between March to September. The trajectories are color-coded with simulated temperature values. Comparison of Sablefish path analysis for individuals released in spawning area 2 (Fig. 5a, eastern GOA) during a high recruitment year (2000) and a low recruitment year as identified by recruitment estimates from stock assessment. See text for description particle day count computation.

Fig. 7. Tortuosity index (Ti) for Walleye Pollock. Trajectory patterns show longer trajectories of individuals than the straight-line distance between starting to ending points for March 2002 (a), compared to more direct trajectories closer to 1 in 2011 (c). Time series of the tortuosity index including seasonal variability (b) and integrated the seasonal variability (d).

Fig. 8. Average temperature (a) and salinity (b) experienced by Sablefish individuals 'spawned' in area 2 in the eastern Gulf (green), and in area 6 in the central Gulf (red). See Fig. 5a for the location of spawning regions.

Fig. 9. Sample trajectories of "winners" (a) and "losers" (b) for the EOF analyses in Pacific cod. 'Winners' are individuals that successfully settled, while 'losers' did not settle or were not retained within the central GOA model grid. The release location of individuals whose trajectories are shown is indicated by the white star. Individuals were released on Feb. 15th, model year 2008.

Fig. 10. Summary of biophysical modes detected by multivariate EOF analysis of normalized (z-scored) life history variables, comparing “winners” with “losers”. Top row: times series amplitude of modes 1 (a) and 2 (b). Middle row: average over all “winning” individuals for each of the life history variables in modes 1 (c) and 2 (d). Bottom row: average over all “losing” individuals for each life history variable in modes 1 (e) and 2 (f). Life history variables analyzed are as follows: larval stage (stage), larval diameter (diam), ambient euphausiids (eup), neocalanus (nca), copepods (cop), vertical mixing intensity (vmix), salinity (salt), temperature (temp), bathymetry (bath), depth (dep), latitude (lat) and longitude (lon).

Fig. 11. The Gulf of Alaska food web, as described by the Ecosim food web model (Gaichas et al., 2010; 2012). GOAIERP focal species and NPZ components are shown in black; functional groups directly connected to a GOIERP group are shown in gray.

Fig. 12. Results (percent change) in species within the Ecosim food web model, resulting from a 10% (equilibrium) increase in the juvenile mortality of the five GOAIERP focal species. Bars display 50%, and lines represent 95% range of variation in Monte Carlo results based on uncertainty in data inputs.

Fig. 13. Important spawning (a) and nursery (b) sites for groundfish in the GOA, identified using IBMs.

Fig. 14. Simplified representation of the Integrated Ecosystem Assessment (IEA) process, as defined for use in NOAA ecosystem-based management efforts (Levin et al., 2009). Modified schematic of the NOAA IEA approach [https://www.integratedecosystemassessment.noaa.gov/]