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Original Article
Making progress on bycatch avoidance in the ocean salmon fishery using a transdisciplinary approach

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Transdisciplinary research that crosses disciplinary boundaries and includes stakeholder collaboration is increasingly being used to address pressing and complex socio-ecological challenges in the Anthropocene. In fisheries, we see transdisciplinary approaches being employed to address a range of challenges, including bycatch where fine-scale data are collected by fishers to help advance spatial approaches in which fishing effort is shifted away from bycatch hotspots. However, the spatio-temporal overlap of morphologically undistinguishable fish stocks, some of which are depleted, is a major concern for some fisheries, including the Pacific Northwest troll Chinook salmon (*Oncorhynchus tshawytscha*) fishery. In this study, we develop and evaluate a transdisciplinary approach to avoid bycatch in the commercial Chinook salmon troll fishery off northern and central Oregon. Based on a unique genetic dataset collected by fishers, fine-scale patterns of stock distribution and spatial stock overlap were assessed. Two hotspots of weak Klamath stock in the study region were identified and related to bathymetry. Results were then fed into a simple bioeconomic model to evaluate costs and benefits of reallocating effort under two scenarios of allowable catch of a weak stock (Klamath). The scenarios demonstrate that effort reallocation could lead to a reduction in Klamath catch as well as to increases in net profit, but outcomes depend on the distance from the fleets' home port to the new fishing area. The output of the model at its current stage should be regarded strategically, providing a qualitative understanding of the types of best fleet strategies. Despite some challenges in transdisciplinarity discussed in this study and the present limitations to incorporate fine-scale changes of Chinook salmon stock distributions in management regulations, we contend that this approach to research has the potential to lead to improved management outcomes.

Keywords: bioeconomic model, Chinook salmon (*Oncorhynchus tshawytscha*), fine-scale spatio-temporal distribution, weak Klamath stock.

Introduction

Many of the problems the world faces, including those related to climate change, food security, and overfishing, are complex and interact across various scientific disciplines and scales (Young *et al.*, 2007; Jerneck *et al.*, 2010). The pressing challenge of science in the Anthropocene is to span disciplinary boundaries and draw on multiple methods. Complex socio-ecological problems, however, cannot be solved purely by academic endeavour. They require the collaboration and engagement of multiple actors including governmental management units, non-governmental organizations, and the private sector and their different interests, needs, and values (Krohn, 2008). Particularly in sustainability science and marine resource management, the push for more integrated collaborative or so-called transdisciplinary research (TD) has been increasingly acknowledged in recent years (Hirsch Hadorn *et al.*, 2006; Ciannelli *et al.*, 2014). The TD approach, in contrast to multi- or interdisciplinarity, is the most integrated form of research (Stember, 1991) with the aim to not only create new knowledge based on the collaborative integration of social and natural disciplines but also to develop a new framework that transcends disciplines by including non-academic participants in the process (Stock and Burton, 2011).

The participatory TD approach has contributed to advances in the effectiveness of many aspects of fisheries management, including bycatch mitigation. Bycatch poses a chronic problem in fisheries worldwide due to the spatio-temporal overlap of target and non-target species. As a consequence, fishery managers are regularly forced to restrict or close entire fisheries, resulting in major financial losses and socio-economic hardship (NMFS, 2015a). Such closures have been triggered as a result of bycatch of a range of overfished, endangered, and protected species or stocks (Sylvia and Enriquez, 1994; Murray *et al.*, 2001; Donoso and Dutton, 2010; Beare *et al.*, 2013). A very general problem is the case where a weak or depleted stock (often called a "choke species") is caught together with a strong or abundant stock and the "choke quota" is reached faster than the target quota, resulting in lower revenues for fishers. The economic and ecological costs of bycatch have spurred research and development with a strong focus on gear modifications to reduce unwanted catch. Key examples of such technical measures are sea turtle and fish excluder devices in trawls, pingers and glow sticks for gillnets, float ropes on lobster traps, and circle hooks on longlines (Gilman, 2011; Little *et al.*, 2014; Roe *et al.*, 2014). However, gear improvements are often poorly suited to address more complex bycatch problems such as in the North Sea mixed fishery (Nielsen *et al.,* 2013) or in the Pacific salmon fishery, the latter targeting multiple stocks that are visually indistinguishable (Utter *et al.*, 1992). As an alternative, spatial approaches have been developed where fishing effort is shifted away from vulnerable stocks altogether, using fine-scale and near-real time information on potential bycatch "hotspots" (Haynie *et al.*, 2009; Eliasen, 2014; Little *et al.*, 2014; O'Keefe *et al.*, 2014; Oliveira *et al.*, 2014; Roe *et al.*, 2014). Hotspot mapping capitalizes on advances in geospatial information systems by using fishers' own catch data to identify areas of high bycatch then communicating this information back to the fleet to avoid these areas. Thus, working together and sharing the information of bycatch, hotspots can help them fish more efficiently. The Pacific whiting (*Merluccius productus*) fleet used this approach successfully, where salmon bycatch was preventing them from fully exploiting its whiting quota (Gilman *et al.*, 2006). Similar approaches are now being implemented in many fisheries, including the Atlantic sea scallop (*Placopecten magellanicus*) fishery where yellowtail flounder (*Pleuronectes ferruginea*) is a choke species (O'Keefe and DeCelles, 2013).

Spatial approaches to bycatch management would also be useful is the USA and Canadian commercial ocean troll fishery for Chinook salmon (*Onchorhynchus tshawytscha*). Here, bycatch does not consist of another species, but rather of weak, threatened, or endangered stocks of the same species. This is problematic because fishers cannot easily distinguish between healthy and depleted stocks by sight, making gear modifications or selective release of bycatch stocks difficult. Many of the North American West coast Chinook salmon stocks have declined substantially in recent decades to only a fraction of their historical abundance. Seventeen Pacific salmon stocks are now listed as threatened or endangered. The dilemma has forced fisheries managers to restrict and, at times, close ocean fisheries off the coasts of California, Oregon, and Washington in the last three decades. Enormous costs to the fishing industry and coastal communities have resulted from these closings, and since 1992, the US government has declared nine disasters related to the salmon fisheries on the West coast (excluding Alaska), paying out US$276.1 million (NMFS, 2015a). The major constraint in this fishery is the inability to identify individual stocks and their local distributions. Average stock distributions at a coarse scale (1 month, 100 km) are known from coded-wire tag (CWT) data collected over the past 40 years (e.g. Weitkamp, 2010). These data are based on hatchery-origin fish with the assumption that these tagged and often more abundant stocks can be used as proxy for untagged stocks, which can be made up of natural-origin fish with or without additional hatchery supplementation. For all but the most abundant and heavily marked stocks, CWT recoveries are too few to resolve distributions at scales finer than month and area (Flaherty, 2015). Tissue samples for genetic stock identification (GSI) have been collected from salmon landings for many years (Winans *et al.*, 2001), but only recently have fine-scale data on all Chinook salmon stocks become available through the use of at-sea sampling by fishers and GSI (Satterthwaite *et al.*, 2014; Bellinger *et al.*, 2015). This now allows the identification of hotspots based on stock-specific distributions in the open ocean including weak, untagged stocks. Ideally, from knowledge of the fine-scale distribution of weak stocks and their potential environmental drivers, alternative management strategies can be developed that are both ecologically and economically sustainable.

In our study, we further develop a TD approach to avoid bycatch in the commercial Chinook salmon troll fishery off northern and central Oregon. We demonstrate how at-sea data collected by fishers, combined with GSI, can be used to create statistical tools to identify (i) fine-scale effort and stock distributions over time, (ii) potential drivers of stock distributions, and (iii) spatial overlaps of weak and strong stocks. Combined with economic data provided by fishers and managing agencies, we fed our statistical results into a generalized and simplified bioeconomic model used to explore multiple management options that potentially maximize net profits of fleets. Outcomes of the statistical and bioeconomic modelling approaches are evaluated in the context of their potential application in management, communication challenges, and implications for the development and application of TD research programmes.

Material and methods

Case study description

The TD dimension of this study is in the integration of natural and human sciences, combining genetics, ecology, oceanography, and economics within a statistical and numerical modelling framework. This approach allows new insights into stock-specific distributions, spatial stock overlaps, oceanographic drivers, and how this information could result in harvest and management strategies that align conservation and reduce fishery restrictions. Statistical and bioeconomic models were developed by a team of economic, social, and ecological scientists. Stakeholder participation was provided in the sampling scheme and during the study when contributing input about fleet behaviour and economics. The intent of this project is to provide analysis back to fishers and managers with the expectation that their behaviour could be altered in a way that benefits both the stocks and the industry. The discrete analyses and modelling steps are described in more depth in the following subsections and supplements. Methods, Results, and Discussion sections are organized by the study progression: identifying (i) the stock distribution, (ii) potential drivers, (iii) stock overlaps, and (iv) alternative management or fisher behaviour strategies.

Our study builds on an existing project that applies genetics, oceanography, and information technology to commercial ocean salmon fisheries. Due to the great challenge for fishers to avoid weak stocks that are morphologically indistinguishable from other target stocks, many partners came together in 2005 to form the Collaborative Research on Oregon Ocean Salmon project and the Washington/Oregon/California West Coast Salmon Genetic Stock Identification collaboration. The aim was to develop more adaptive strategies for salmon management through the use of fine-scale sampling at sea, combined with GSI. These efforts were motivated by projected fishery restrictions due to low abundance of Klamath fall Chinook and represented a unique research effort involving fishers, scientists, managers, and policy-makers. The salmon troll fishers were heavily involved in the project and provided geo-referenced catch and fishing effort data and conducted at-sea sampling for the GSI analysis carried out later by university or National Oceanic and Atmospheric Administration (NOAA) Fisheries labs. For a detailed description of the at-sea sampling design, see Bellinger *et al.* (2015). Based on this research, descriptions of the ocean distribution of Chinook salmon stocks across the Oregon and Californian coasts during 1–2 years have recently been made using monthly time-steps and nine open areas in California and Oregon as spatial resolution (Satterthwaite *et al.*, 2014; Bellinger *et al.*, 2015), which is roughly comparable with pre-existing management models and analyses based on CTW or other GSI data (e.g. Satterthwaite *et al.*, 2013, 2015).

Our study, in contrast, uses a finer spatial resolution and focuses on the northern Oregon (NO) and central Oregon (CO) coast regions and on fishing fleets from four ports along the coast: Garibaldi, Newport, Winchester Bay, and Coos Bay (Figure 1). New analysis of data for 2010–2013 allowed testing for both seasonal and interannual patterns. Similar to the previous studies, we used a monthly time-scale, which was most feasible for the bioeconomic model. The focus was set on Klamath River fall-run Chinook salmon, which is the harvest indicator for the threatened California coastal Chinook stock (Klamath River fall Chinook are CWT'd while California coastal Chinook are not) and which has been one of the constraining stocks in Oregon and California fisheries. The GSI analyses cannot differentiate between autumn- and spring-run, but as the latter represents not >10% of the Klamath stock (NMFS, 2014) it will

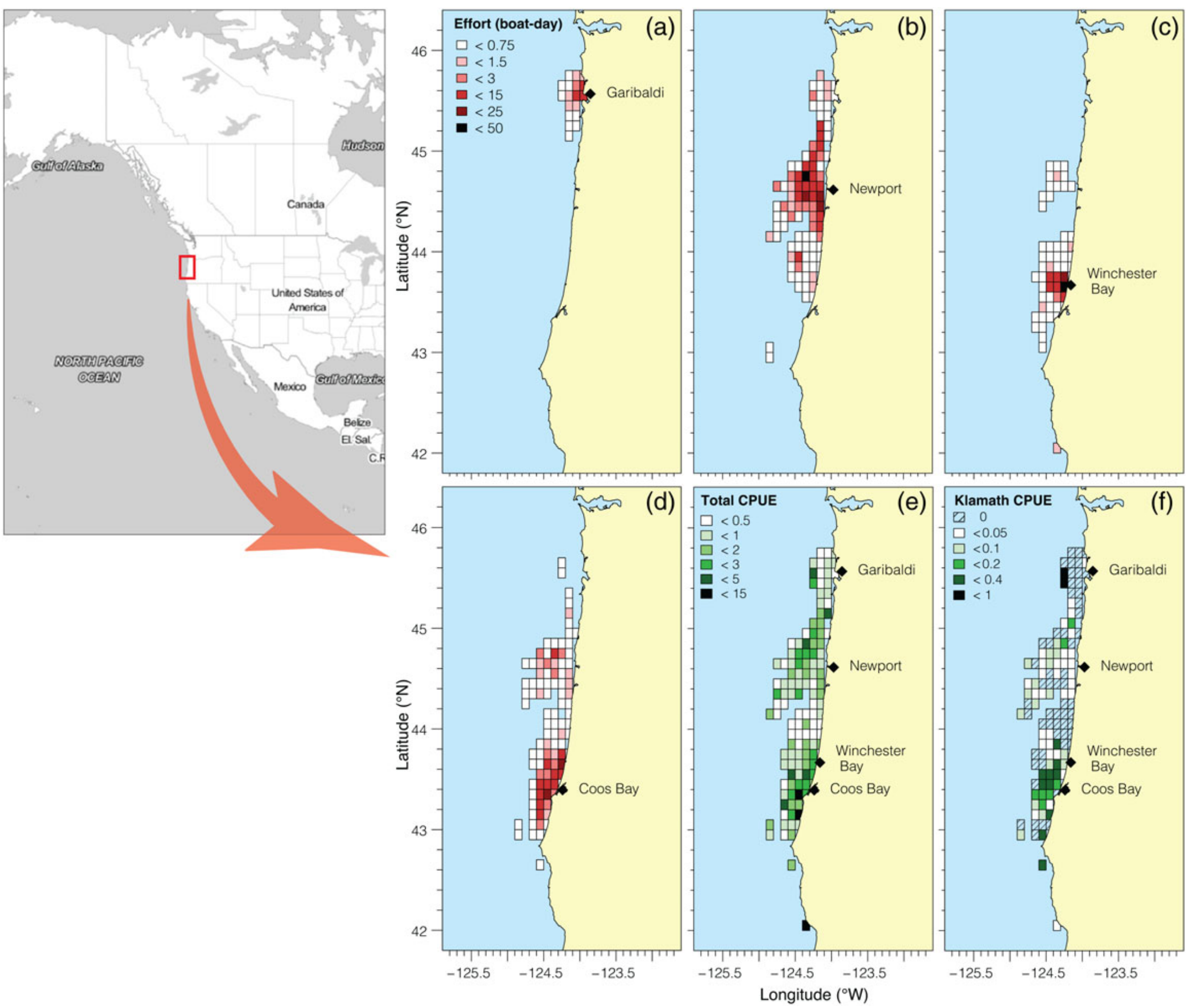

Figure 1. Location of study area. Spatial distribution of mean annual fishing effort individually for the fleet of Garibaldi (a), Newport (b), Winchester Bay (c), and Coos Bay (d). Spatial annual pattern of total catch (e) and Klamath catch (f), both standardized by fishing effort (i.e. unit hour). Each grid cell has a size of 0.1 degree latitude/longitude. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

not change the conclusions of this demonstration. Additional information on fleet behaviour and economics was derived in meetings with fishers.

Spatio-temporal aggregation of effort, catch, and environmental data

The track log and catch data collected by fishers represents about 15% of the entire Chinook salmon ocean troll fishery in the NO and CO areas. The data used in this study summarize a total of 850 fishing trips of the four fleets and cover the main fishing season from May to September in 2010–2013 (except September 2011). The Garibaldi fleet, in general, is less active fishing and is also inconsistently sampled leading to sample data that are an incomplete representation of its fishery.

To estimate levels of effort and catch at a fine spatial scale for our spatio-temporal analysis and bioeconomic modelling, data were aggregated to a regular grid of 0.1 decimal degree latitude/longitude ($\sim$11 $\times$ 8 km or 7 $\times$ 5 miles), which gave us a total of 167 grid cells with recorded effort and 126 grid cells with at least one recorded Chinook salmon catch. This grid size represented a compromise between fine spatial scale, computationally feasible number of cells for the bioeconomic model, and the avoidance of binary data for rare species such as Klamath (97% of all cells had catches $<$10 at the current resolution). Monthly fishing effort per grid cell and fleet was calculated by first assigning each track record to a grid cell based on its coordinates, then adding up the fishing time of each of these track records and converting the time to unit day. The time-intervals between each record of an individual boat were usually 5 min during active fishing. If time-intervals were much $>$5 min, this indicated steaming time. Vessels need to steam to the fishing area to catch the fish, which needs to be considered in the fuel costs. To estimate the total monthly effort for each fleet and grid cell spent on fishing and steaming, a proxy for steaming effort was added to the calculated monthly fishing effort. The distance from the fleets' home port to the centre of each grid cell was converted into time in days by assuming an average vessel speed of seven knots. Individual salmon catch was similarly assigned to each grid cell then aggregated, depending on the analysis, by month, year, fleet, or identified stock. Catch data for all statistical analyses were converted into catch per unit effort (CPUE) or into biomass.

For the analysis of the Klamath stock distribution, bathymetric and geospatial parameters were used including mean bottom depth per grid cell, the depth range within each cell (as an indicator for slope), the distance from the grid cells' centre to the nearest shoreline, and distance to the mouth of the Klamath River. Sea surface temperature (SST) was used as an indicator for hydrological conditions. Data were downloaded from the NOAA ERDAP data server (Multi-scale Ultra-high Resolution SST analysis fv04, Global, 0.011 Degree, Daily) and aggregated to monthly means per grid cell.

Spatio-temporal distribution modelling

To understand the fine-scale spatial dynamics of Klamath and other Chinook salmon stocks in the NO and CO regions, the annual and monthly distributional patterns of fleet-specific fishing effort and Klamath and total catch, standardized by fishing effort, were first identified. For each genetically identified stock, the distributional centre of gravity (i.e. the midpoint of the distribution calculated by weighting the mean coordinates of each grid cell with the stock-specific CPUE) over the entire study period was computed. To identify potential oceanographic drivers for locally higher Klamath catches (standardized as CPUE), we applied a two-step modelling approach due to the large numbers of zeros in the data ($>$80%), which can cause biased parameter estimates and standard errors and excessive overdispersion (Zuur *et al.*, 2009). In the first step, only the zeros and non-zeros were considered and a binomial generalized additive model (GAM) on the full dataset applied (i.e. all grid cell, month, and year combinations were sampled where fishing took place) to model the probability that non-zero CPUE is observed. In the second step, we modelled only the non-zeros using a GAM on the ln-transformed CPUE data assuming a normal distribution. This approach is similar to a hurdle model or a zero-inflated Poisson model, although we did not differentiate between different types of zeros as the latter does (Zeileis *et al.*, 2008). Explanatory variables in both modelling steps included the time components year and month, SST, and geospatial and bathymetric variables distances to coast and Klamath River mouth, mean bottom depth, and ln-transformed depth range. For a detailed description of the 2-step model, see supplementary material.

Potential associations or co-occurrences of Klamath with other stocks were studied by testing for significant overlaps in space and time using a modified spatial overlap index (*SOI*) (Williamson and Stoeckel, 1990):

$$SOI_{my} \frac{\sum_{z=1}^{n} (K_{gmy} \times X_{gmy}) \times n}{\sum_{z=1}^{n} (K_{gmy} \times \sum_{z=1}^{n} X_{gmy})}, \qquad (1)$$

where g represents the grid cell, m and y are month and year, respectively, and n is the number of grid cells where fish were sampled in the particular year and month combination. The variable K is the Klamath CPUE in a given grid cell and X is the CPUE of another stock in the same grid cell. Because fishing effort was not evenly distributed across the area, catch was standardized to CPUE. An overlap index of $<$1 indicates spatial separation between Klamath and the other specific Chinook stock, an index = 1 represents a uniform or random distribution, while values $>$1 indicate an aggregation of both stocks in certain grid cells. To evaluate whether the observed overlap in each month could have been obtained by chance, consistencies of *SOI* values between month and year were assessed. A two-way multivariate analysis of variance (MANOVA) (Cramer and Bock, 1966) was applied in which stock-specific *SOI* values were treated as multivariate-dependent variables and month and year as independent variables. The MANOVA approach allowed testing for both the multivariate effect (the effect of year and month on the spatial overlap of the combined stocks) as well as univariate effects (whether stock-specific *SOI* values were consistent between months and years). Since there were no replicates for each year–month combination, interactions could not be tested. The number of stocks included had to be limited to 10 because of the small number of years and months; hence, only stocks with a general high overlap (overall *SOI* mean $\geq$2.0) were included. The univariate effects, which describe the effects of month and year against each stock separately, were examined after the multivariate analysis by applying a series of two-way ANOVAs on each of the 10 stocks. Three further stocks that had a similar higher overall mean *SOI* ($\geq$1.5) and that belonged to the most abundant stocks were included in the individual ANOVAs where sample size was not limiting their inclusion. For information on model diagnostics, see Supplementary data.

In addition to assessing the spatial overlap in geographical space, the difference between capture depth of Klamath and other stocks was tested using the original catch data. This information was useful to assess if Klamath catch could be avoided by fishing at a different depth. First, a three-way ANOVA with capture depth as response variable and the identified stocks, month, and year as explanatory variables was performed, including a three-way interaction term between stock, month, and year and their respective two-way interactions. After identifying significant ($p < 0.05$) two- and three-way interactions, 19 individual ANOVAs for each month and year were applied followed by a series of *post hoc* analyses (Tukey's "honest significant difference"). All data analyses and spatial distribution maps were conducted using the free software environment for statistical computing and graphics R (version 3.2.0) (R Core Team, 2015). To account for the inflated type I error rate due to multiple testing in all individual ANOVAs and partial violations of the homogeneity assumption, p-values were adjusted using Holm's correction method (Holm, 1979).

Bioeconomic modelling

We developed a dynamic bioeconomic model that incorporates results from the spatio-temporal modelling to evaluate how changes in effort allocation could help reduce catches of weak Klamath while keeping the fishers' profit at a maximum. The model reflects a fishery system in which the profit earned by the fleets is the main driver (Figure 2). Effort allocation is determined both by the fish stock distribution and economic conditions (e.g. revenues and fishing costs). Management regulations, implemented in the model as constraints to catches of weak stocks, alter the relative profitability and hence subsequent effort decisions by fleets, which, in turn, impact the fish stocks. Our model builds heavily on the models developed by Salz *et al.* (2011) and Simons *et al.* (2014a), which unlike previous models (e.g. Naqib and Stollery, 1982; Da Rocha *et al.*, 2010), not only consider possible effort redistributions but also include multiple interacting factors and feedbacks (for a detailed description, see Salz *et al.*, 2011; Simons *et al.*, 2014a). The presented model, however, is simplified in the sense that we did not include age-structured population dynamics or stock–recruitment relationships. It is primarily a strategic tool that provides a qualitative understanding of relative changes under various management scenarios. The individual model components are described in more detail in the following sections.

The economic component in the model computes gross revenues for each of the four fleets based on the value of landings of target stocks (the landings of not explicitly modelled stocks are included as fixed percentages) (Figure 2). Net profit of a fleet is calculated as the difference between gross revenue and the sum of economic costs (fuel, other variable, crew, and fixed costs). Fixed costs are directly proportional to the number of vessels, while variable costs are dynamic and are associated with variations in total effort. Profit, furthermore, depends on the interest rate for capital invested in the fleet. Based on past patterns of effort and stock distribution, the applied CONOPT solver (for a detailed description of the CONOPT algorithm, see Drud, 1991) finds for the following year the optimal effort pattern (number of fishing days and its spatio-temporal distribution), within the observed minimum and maximum fishing effort, that maximized the total net profit of all four fleets. If the solver finds more than one optimal effort, the lower effort level is used.

The optimal effort pattern is used in a standard Cobb–Douglas production function (see Salz *et al.*, 2011; Simons *et al.*, 2014a) to calculate catch, which is then used to estimate stock size and revenue, given the observed fish price (Figure 2). The Cobb–Douglas function links the biological and economical model component and was chosen as it assumes that fishing mortality is not directly proportional to effort and yield is not proportional to stock size. Similar to Salz *et al.* (2011), the fish population is described by a single variable, interpreted as catch biomass, and modelled by a simple logistic growth function (see Supplementary Table S2) accounting for seasonal changes in the various stocks and changes in their spatial distribution (at the level of selected grid cells). Population dynamics of salmon are a function of spawner abundance, life history traits, and freshwater and marine environmental conditions (Healey, 1983; Greene *et al.*, 2005) and must be modelled at the stock level. Rigorous modelling of population dynamics was beyond the scope of this study. The logistic growth model serves as a placeholder for the biological component in the model.

The fishery system in the model is dynamic in a way that profit from 2 years ago determines the level of investment or disinvestment in the fleets (see Salz *et al.*, 2011; Simons *et al.*, 2014a), involving changes in the number of vessels per fleet. Given that free access in the fisheries is allowed, any fleet that is highly profitable will become bigger, and hence the profit of the individual vessels would dissipate in the long run. In reality, the investment/disinvestment function (number of vessels) is based on future expectation, but because of lack of information, the past profitability is used in the model. Changes in fishing behaviour in terms of effort allocation patterns or entry and exit of vessels consequently affect fleet economics and the local total stock size in the next time-step.

Modelling input data

For the bioeconomic model, the following data were compiled: effort, landings weight and value, fuel consumption and costs, variable (e.g. ice, crew, food supplies) and fixed (e.g. insurance, boat maintenance, moorage fees) costs, number of vessels, sea-days, and revenues for the years 2010–2013. As input for the model, the average of these years was used (see Supplementary Table S1). The landings weights were based on the Oregon monthly troll Chinook average dressed weights taken from the latest ocean salmon fisheries report (PFMC, 2015). Landing values were based on the average monthly ex-vessel troll salmon price (in US$) per dressed pound for Oregon taken from each of the annual ocean salmon fisheries reviews (PFMC, 2012, 2013, 2014, 2015). Effort data were made up of steaming and fishing effort per grid cell/month. Biological data were the total catch number and biomass per grid cell/month as well as the proportion of Klamath from the total catch per grid cell/month.

Scenarios

Model calibration was based on average economic, effort, and catch data for 2010–2013. After the calibration, we ran the model simulation for the next year under the following two scenarios:

1. Optimal harvest scenario (ScenOpt): A harvest strategy where the optimal allowed catch of Klamath and other modelled salmon stocks is calculated via a Baranov catch function.
2. Constrained harvest scenario (ScenConst): A harvest strategy where the optimal allowed catch of Klamath (the constraining stock) is reduced by 50% (hence the allowed Klamath catch represents half of the Klamath catch from ScenOpt). The allowed catch of other stocks is simulated in the same way as in ScenOpt.

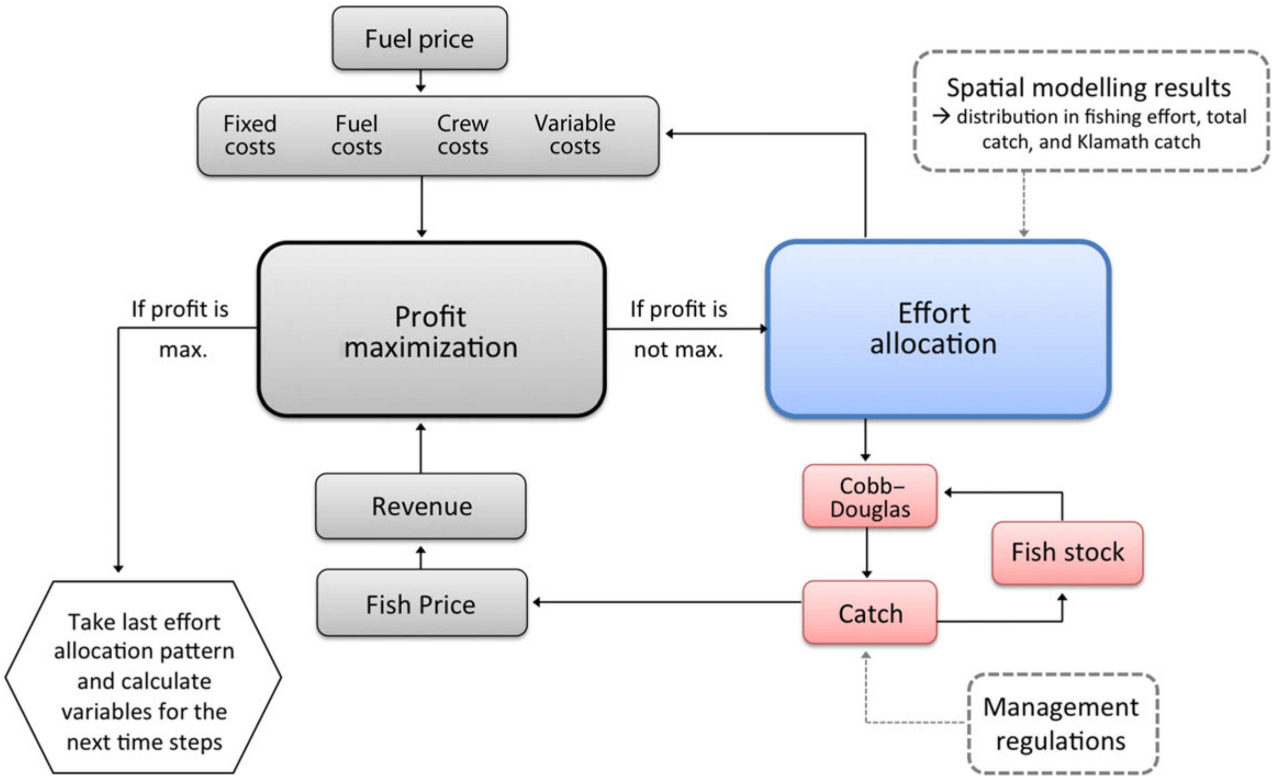

Figure 2. Conceptual model design with arrows that explain the interaction between effort allocation and economic and biological submodules. In the maximization procedure, the effort allocation pattern is changed until profit of the entire fleet is maximized. When profit is maximized, the last effort allocation pattern is used in the Cobb–Douglas function to calculate catch, which in turn is used to calculate stock size, costs, and fleet size adjustment for the next step. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Table 1. Port-specific sampled fishing effort per year and each month of the fishing season, averaged across the period 2010–2013 (mean and s.e. is provided).

	Fishing effort in boat days (i.e. 8 h)						Annual catches in number	
Port	Annual	May	June	July	August	September	Total	Klamath
Garibaldi	27 ± 22	2 ± 1	11 ± 7	3 ± 3	11 ± 10	0 ± 0	58 ± 48	1 ± 1
Newport	267 ± 115	62 ± 31	96 ± 34	35 ± 13	57 ± 27	17 ± 9	1463 ± 710	38 ± 18
Winchester Bay	141 ± 52	25 ± 13	49 ± 15	16 ± 4	40 ± 16	12 ± 6	687 ± 338	28 ± 12
Coos Bay	147 ± 49	33 ± 14	49 ± 20	14 ± 4	33 ± 12	18 ± 11	1034 ± 336	50 ± 19

Annual Chinook salmon catch is presented for all stocks and Klamath in specific.

Based on these two scenarios, an optimal fishing effort distribution was modelled on a monthly time-step, while profit maximization, calculation of costs, and the fleet size adjustment were modelled on an annual scale. Any potential changes in the Chinook salmon distribution due to environmental changes during the predicted year cannot yet be taken into account by the model.

Results

Distributional patterns at fine spatial scales

The annual distribution of sampled fishing effort of all four fleets within the NO and CO regions shows a clear pattern of home port attachment (Figure 1a–d). All fleets fished most intensively near their home port then decreased effort with increasing distance from port. The Garibaldi fleet showed the strongest localized pattern with the lowest sampled fishing effort per year (27 ± 22 boat-days) (Table 1). Newport had the highest annual sampling effort with 267 ± 115 boat-days, mainly concentrated right at the coast and offshore of Newport, but stretching north to Garibaldi and south to Winchester Bay. Consequently, the Newport fleet caught the highest number of Chinook salmon per year (Table 1). The two fleets of the closely located ports Coos Bay and Winchester Bay fished at similar intermediate levels, although Coos Bay spanned its fishing range much farther north and sampled on average 50% more Chinook salmon than Winchester Bay. This effort pattern, though, was not consistent over time. First, all fleets showed great differences in sampled fishing effort between months (Table 1) but also between years of the same month as indicated by the high standard errors. Second, the sampled fishing effort varied spatially between months, as indicated in Figure 3, and between years. Much of this variability reflects the distribution of sampling effort rather than differences in fleet behaviours.

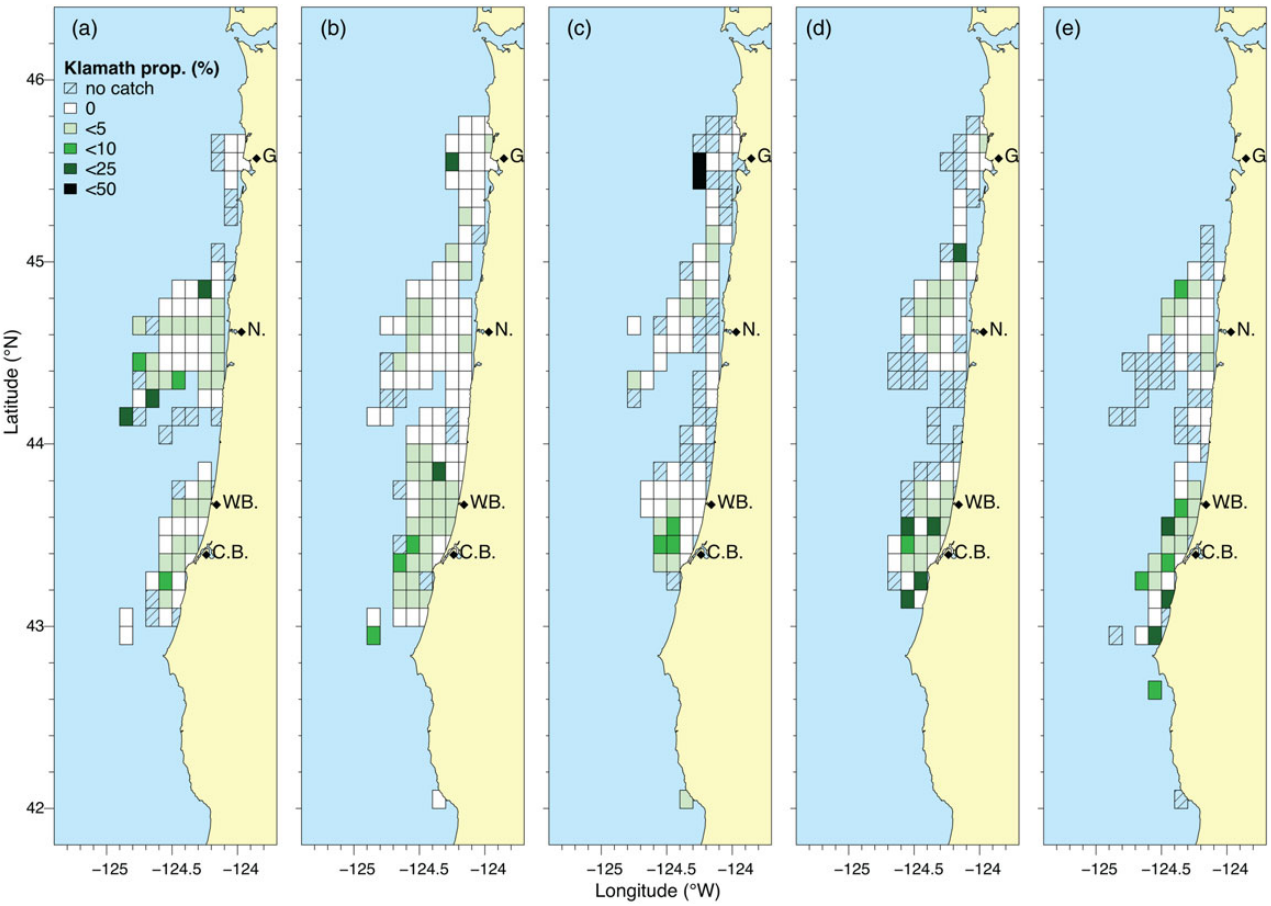

Figure 3. Changes in catch proportion of Klamath vs. total catch between the different months of the main fishing season (averaged across the study period 2010 – 2013): (a) May, (b) June, (c) July, (d) August, and (e) September. Each rectangle represents an area where actual fishing of all fleets together took place. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

The mean annual distribution of sampled catch standardized by fishing effort shows two core regions where salmon were mainly caught, one near Coos Bay and one offshore of Newport (Figure 1e). Particularly near Coos Bay, catch rates were up to six individuals per boat-hour or more, while in many grid cells catch rates were <2 per boat-hour. High catch rates, in combination with the fishing effort, explained the high catch numbers by the Newport and Coos Bay fleets. The Klamath stock showed a similar distribution as the overall stock pattern with high aggregations near Coos Bay and offshore Newport (Figure 1f). However, Klamath aggregated more strongly near Coos Bay, with up to 10% of the total sampled catch in various grid cells. This coarse-scale aggregation was also consistent across months, whereas at a fine scale, i.e. at the grid cell level, the proportional distribution varied slightly. Because of the strong aggregation near Coos Bay, highest numbers of Klamath were caught by the Coos Bay fleet with on average 5% of the total catch (Table 1).

Drivers of spatial Klamath distribution

The two-step GAM analysis of potential oceanographic drivers for Klamath occurrences based on binomial and presence-only data (CPUE >0) demonstrated the importance of geospatial and bathymetric features. Catches of Klamath (i.e. non-zero CPUE values) were best explained by a positive linear slope effect (represented by the ln-transformed depth difference within each grid cell) as well as by non-linear effects of distance to coast and mean depth (Figure 4a–c). Here, catch probabilities generally declined with increasing distance to the nearest coast. Beyond a distance 40 km, however, probabilities started to increase again. In contrast, mean depth had a strong positive effect, which reversed at depth levels >150 m. The overall probability of Klamath catches differed slightly between the various months and years (interaction term month $\times$ year: $p = 0.013$). Despite the strong significant effects, the tested variables could only explain 16% of the variability in Klamath catches, indicating other environmental drivers being more important.

Higher CPUE of Klamath (ln-transformed) can generally be found at greater depth and a distance of 300 km to the river mouth entrance (Figure 4d and e). The depth effect, in contrast to the binomial GAM, is hereby constantly positive, also beyond 150 m. While the slope had strong positive effect on catch probabilities, higher CPUE were instead related to lower slope levels (Figure 4f). These static variables, after all, only explain 21% of the CPUE variance. The best model also included month, year, and their interaction term, which increased the explanatory power to 41%.

No significant relationship was found for SST, which indicates that monthly mean SST is not a suitable proxy for oceanic conditions affecting Klamath catch distribution at this scale.

Overlap of stock-specific distributions

The *SOI* analysis shows that Klamath overlapped spatially (overall *SOI* mean ≥ 1.5) with 13 of the 22 stocks that have been genetically

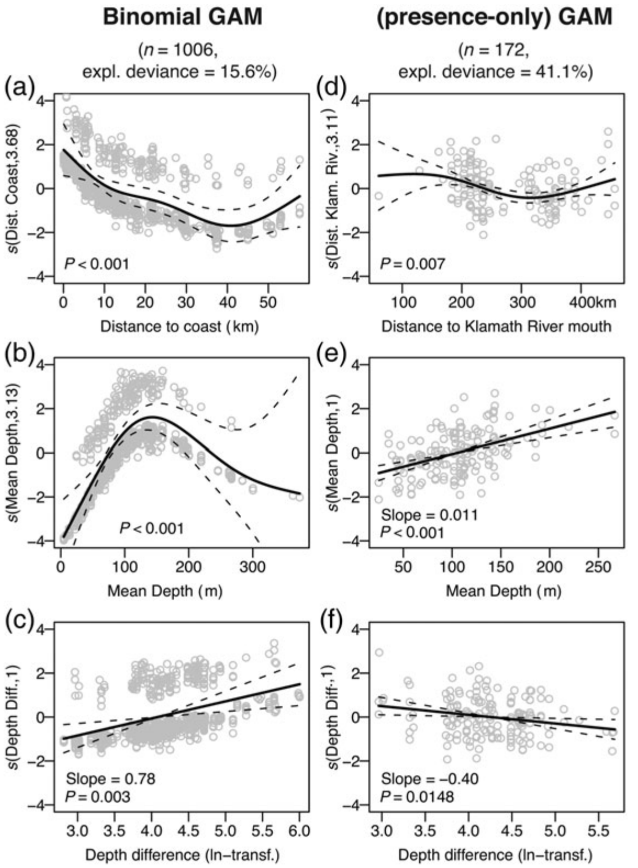

Figure 4. Partial effect plots from the two-step model approach, i.e. from the final binomial GAM and the final GAM on non-zero CPUE values of Klamath (assuming a Gaussian distribution) showing the effect of the geospatial (a, d) and the bathymetry variables (b–f). Values on the *y*-axis indicate the effect that the term on the *x*-axis has on presence/absence or on the ln-transformed Klamath CPUE. Numbers in parentheses on the *y*-axis indicate the estimated degrees of freedom (e.d.f.). If the e.d.f. is 1, i.e. linear effect, the respective estimated coefficient is presented. Solid lines indicate the smoothed (non-) parametric trend, the dashed lines indicate the lower and upper 95% CI. The points represent the partial residuals.

identified (Table 2). This general overlap pattern was consistent across months and years as indicated by the statistically insignificant MANOVA effects (month: Pillais' Trace = 2.5, $F(4,11) = 0.85$, $p = 0.67$; year: Pillais' Trace = 2.3, $F(3,11) = 1.3$, $p = 0.31$). Also the univariate analysis indicated that monthly *SOI* values did not differ significantly over time for any of the 13 stocks (see Supplementary Table S3). Comparing the overall centre of gravity of Klamath with the co-occurring stocks showed that Rogue, weak California coastal stock, and abundant Central Valley fall stock had a more southerly distributional centre than Klamath, whereas the others, including weak Snake fall and Lower Columbia fall stocks, had a more northern centre of gravity (Table 2). This suggests that higher catch of Klamath in the south is more likely to be associated with catch of California stocks, particularly Central Valley fall, whereas Klamath catch in the north is likely to go with higher catch of the other ten stocks. The nine stocks that showed little or no overlap with Klamath were centred in their distribution farther north than Klamath, except for Central Valley winter and spring stock which were caught almost exclusively in California.

Klamath overlapped similarly in its depth distribution with the 13 co-occurring stocks. Although some of these stocks had on average a greater monthly mean capture depth, differences were mostly not strong enough to be significant when conducting *post hoc* comparisons after significant stock effects in individual one-way ANOVAs were detected for certain month–year combinations (Table 3). Snake fall and Lower Columbia spring and fall runs in 1–3 months were the only exception with significant differences in the mean capture depth compared with Klamath. Consequently, in areas where Klamath is abundant, fishing outside the Klamath depth range to target other co-occurring stocks might lead to lower total catch.

Costs and benefits of potential options for bycatch avoidance

Our bioeconomic modelling output shows that all three fleets together could reduce Klamath bycatch by 30% by changing effort allocations under ScenConst. Results of the Garibaldi fleet are not presented here as the inconsistent sampling produced unrealistic model outcomes, i.e. no changes of any economic variable and effort pattern under the two model scenarios. Under ScenConst, the model predicts reduced Klamath catch for the year 2014 while maintaining a high net profit. In this scenario, fishing effort generally decreased up to 80% or more around Coos Bay and offshore of Newport where Klamath fish are mainly located (Figure 5). In contrast, effort can generally increase by >60% farther south of Coos Bay, near-shore at the ports of Garibaldi and Winchester Bay, and from Newport within 30 km of the coast (i.e. four grid cells). The spatial pattern of effort reallocation under ScenConst, nonetheless, varies slightly between fleets as past effort distributions also showed a fleet-specific pattern. Since the Newport fleet fished mainly around their home port, the model suggests that this fleet should reduce effort offshore and increase effort within 30 km of the coast. The same reallocation pattern is suggested for the segment of the Coos Bay fleet that fish intensively near Newport, but this fleet fished even more intensively in the south near its home port where Klamath had its core aggregation area. Consequently, the Coos Bay fleet would need to reduce effort levels by 60–80% or more. For the Winchester Bay fleet, which caught the lowest number of Klamath and other stocks, an effort allocation near and slightly north of their home port as well as in an area south of Coos Bay shows lower Klamath catch rates. On the other hand, effort just south of their home port should decrease. The effort reallocation pattern for individual fleets on an annual scale is not much different from the monthly results (Supplementary Figure S1). The most pronounced differences were found for the Newport fleet, which would benefit by reducing fishing effort north of its home port later in the year and maintaining low effort near port in July and August. The suggested reductions in effort levels south of Winchester Bay are most important for its fleet in June, August, and September (Supplementary Figure S1).

The predicted reduction in Klamath bycatch based on the described effort re-allocations under ScenConst has different economic consequences for the three fleets. The small changes in effort allocation suggested for the Winchester Bay fleet lead to small decreases (<4%) in total catch but also reduced fishing effort and thus cost, which in turn decreases revenue and net profit at similar levels (Figure 6). On the other hand, shifting the fishing effort just slightly north of the Klamath hotspot reduces the Klamath catch by 33%. A similar reduction could be obtained for the Newport fleet while increasing net profit by 10%. The shift

Table 2. Stock-specific summary of caught individuals, spatial overlap with Klamath, mean capture depth, and average location of the stock averaged across the entire period, i.e. for the study period 2010–2013 and the months May–September.

	Chinook salmon stock	Annual number of sampled individuals (mean ± s.e.)	Monthly *SOI* (mean ± s.e.)	Monthly mean capture depth (mean ± s.e. in m)	Centre of gravity of stock-specific CPUE, averaged across entire period (latitude/longitude in decimal degree)
1	Alaska	2 ± 1.2	0.4 ± 0.18	92 ± 3	44.541°N 124.373°W
2	**BC Mainland/Vanc. Is.**	**12 ± 6.5**	**2.8 ± 1.20**	**74 ± 6**	**44.218°N 124.357°W**
3	**Fraser and Thompson**	**43 ± 17.7**	**2.6 ± 0.69**	**72 ± 4**	**44.521°N 124.368°W**
4	Puget Sound	94 ± 43.3	1.2 ± 0.28	68 ± 5	44.452°N 124.345°W
5	**Washington Coast**	**10 ± 3.7**	**3.0 ± 0.95**	**71 ± 7**	**44.434°N 124.367°W**
6	**Lower Columbia Spring**	**14 ± 7**	**2.0 ± 0.84**	**68 ± 5**	**44.466°N 124.349°W**
7	**Lower Columbia Fall**	**357 ± 175.7**	**2.2 ± 0.66**	**65 ± 4**	**44.245°N 124.359°W**
8	Mid Columbia Tule	306 ± 126.7	0.9 ± 0.25	63 ± 4	44.379°N 124.298°W
9	Mid-Upper Columbia Spr	2 ± 2.2	0.3 ± 0.17	62 ± 5	43.976°N 124.387°W
10	**Upper Columbia Su/Fall**	**377 ± 150.4**	**1.9 ± 0.28**	**68 ± 3**	**44.202°N 124.371°W**
11	Snake Spring/Summer	1 ± 0.5	0.1 ± 0.04	93 ± 8	44.383°N 124.25°W
12	**Snake Fall**	**128 ± 38.4**	**1.5 ± 0.40**	**73 ± 6**	**44.324°N 124.355°W**
13	Willamette	12 ± 5	0.8 ± 0.64	57 ± 3	44.238°N 124.347°W
14	Deschutes Fall	54 ± 21.5	1.4 ± 0.36	66 ± 6	44.318°N 124.355°W
15	**North Oregon Coast**	**33 ± 12.7**	**3.4 ± 1.21**	**74 ± 6**	**44.476°N 124.374°W**
16	**Mid Oregon Coast**	**383 ± 89.9**	**2.2 ± 0.36**	**74 ± 5**	**44.026°N 124.419°W**
17	**Rogue**	**123 ± 28.7**	**2.6 ± 0.53**	**80 ± 5**	**43.89°N 124.438°W**
18	N. CA/S. OR Coast	16 ± 4.4	4.1 ± 1.72	93 ± 6	44.105°N 124.416°W
19	Klamath	116 ± 38.7	/	72 ± 6	43.976°N 124.429°W
20	**California Coast**	**14 ± 4**	**2.4 ± 0.75**	**91 ± 5**	**43.941°N 124.509°W**
21	Central Valley Spring	18 ± 11.7	1.1 ± 0.46	65 ± 6	43.819°N 124.394°W
22	**Central Valley Fall**	**1128 ± 559.7**	**1.8 ± 0.3**	**66 ± 4**	**43.896°N 124.359°W**
23	Central Valley Winter	0.5 ± 0.3	0.3 ± 0.19	52 ± 6	43.7°N 124.25°W

Stocks are ranked based on their origin from north to south. Bold typing indicates stocks that show a high overlap with Klamath (i.e. $SOI \geq 2$) and were further used in the statistical analysis of *SOI* and capture depth overlap through time.

Table 3. One-way ANOVA of capture depth between Klamath and the 13 stocks that had a high spatial overlap with Klamath (i.e. $SOI \geq 1.5$).

		Individual one-way ANOVA		Tukey's HSD		
Y	**M**	**F**	**Adj. *p***	**Pairwise comparison Klamath vs.**	**Mean diff.**	**Adj. *p***
2010	5	$F_{(13,274)} = 2.93$	**0.01**			
2010	6	$F_{(13,650)} = 4.69$	**<0.001**	L. Columbia Fall	23.8	0.02
2010	7	$F_{(11,\ 237)} = 0.83$	1.00			
2010	8	$F_{(11,\ 443)} = 4.90$	**<0.001**	Snake Fall	−30.18	0.03
2010	9	$F_{(10,\ 108)} = 1.26$	1.00			
2011	5	$F_{(10,\ 214)} = 2.29$	0.13			
2011	6	$F_{(13,\ 1186)} = 5.13$	**<0.001**	L. Columbia Fall	27.1	<0.001
				L. Columbia Spring	50.3	0.04
2011	7	$F_{(11,139)} = 3.21$	**0.01**			
2011	8	$F_{(13,307)} = 1.68$	0.45			
2012	5	$F_{(12,1829)} = 5.95$	**<0.001**	L. Columbia Fall	17.0	<0.001
2012	6	$F_{(11,1175)} = 3.96$	**<0.001**			
2012	7	$F_{(12,590)} = 1.31$	1.00			
2012	8	$F_{(13,1530)} = 2.44$	**0.03**			
2012	9	$F_{(13,589)} = 2.03$	0.13			
2013	5	$F_{(7,126)} = 1.85$	0.50			
2013	6	$F_{(11,323)} = 0.60$	1.00			
2013	7	$F_{(10,320)} = 3.16$	**0.01**			
2013	8	$F_{(9,215)} = 4.28$	**<0.001**			
2013	9	$F_{(13,526)} = 1.31$	1.00			

ANOVAs were performed individually for each month and year. When stock differences were significant (<0.05, marked in bold; *p*-value adjusted by the Holm method), pairwise comparison between Klamath and all other stocks were performed *a posteriori*. Only significant results from Tukey's "honest significant difference" test are presented.

in effort to a region less inhabited by Klamath allows a 19% increase in effort, which increases fuel costs at similar levels, but at the same time is predicted to lead to higher total catch of ~11%, which ultimately results in a net financial benefit. Reduction in Klamath catch was greatest for the Coos Bay fleet with 67%, but because of their proximity to the main Klamath area, this was only obtained in the model by a great reduction in overall fishing effort (26%). Although this would lead to lower fuel, crew, and variable costs, total catch would decline by ~14%, leading to net profits 21% lower than under ScenOpt.

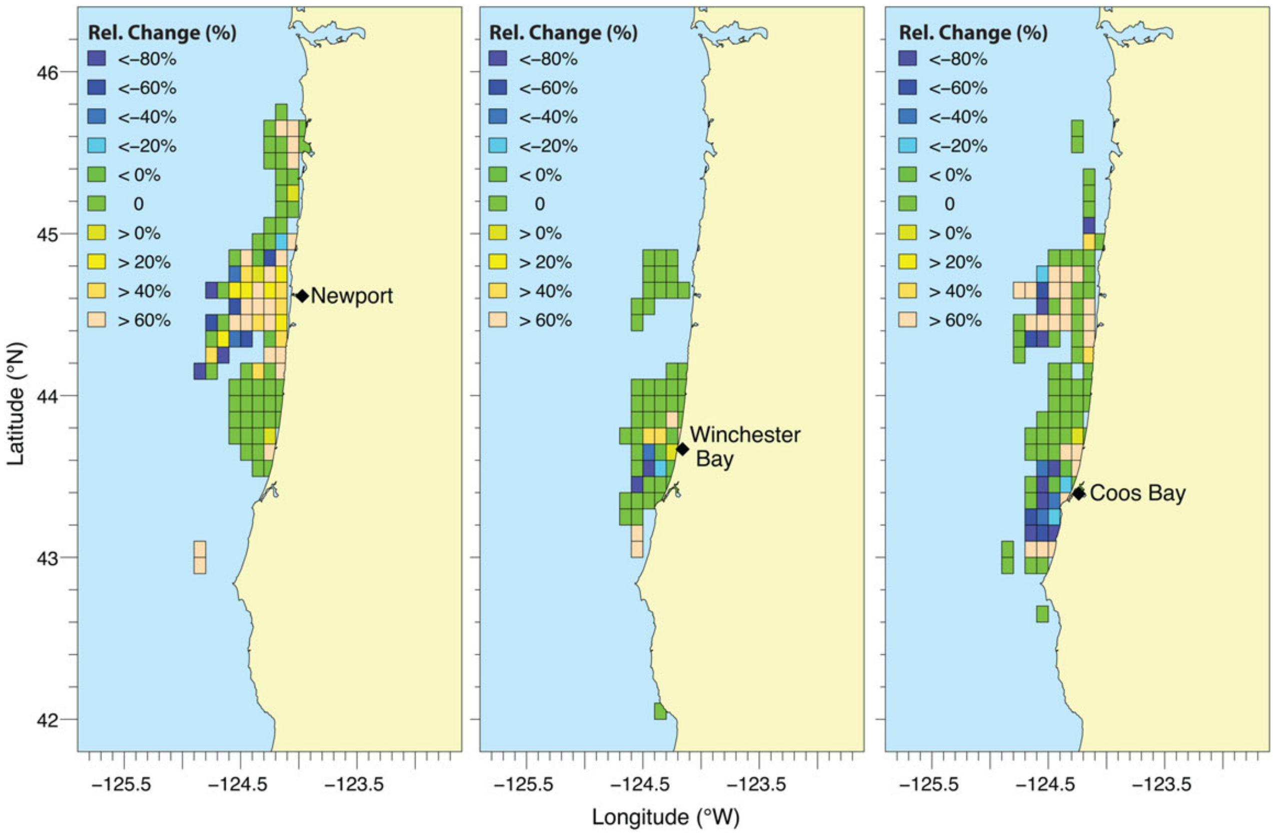

Figure 5. Changes (in %) in total annual effort allocation under ScenConst relative to ScenOpt presented for Newport (left), Winchester Bay (middle), and Coos Bay (right). The maps show the predicted changes for the year 2014. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Discussion

Distribution of Klamath and potential drivers

When focusing on the NO and CO coastal regions, it becomes apparent that the Klamath distribution at a finer-scale is not homogeneous or gradually decreasing with the distance to the natal river. Instead, it shows two hotspots within this less inhabited area. Few studies have looked explicitly at the ocean distribution of Klamath in the California Current System. However, at a broader spatial scale, studies show that fall-run or ocean-type Chinook tend to remain closer to their natal river than stocks with spring-run life histories (Healey, 1983; Weitkamp, 2010) and that southern stocks (i.e. south of the Columbia River) migrate less to the northern regions like the Gulf of Alaska or Bering Sea (Weitkamp, 2010). Two more recent studies (Satterthwaite *et al.*, 2014; Bellinger *et al.*, 2015), based on different analyses of the same GSI dataset, show that Klamath occurs all along the coast with its core region between the northern California Klamath zone and Fort Bragg near the Klamath River mouth. The fact that Klamath aggregated in two areas within this local region indicates that factors other than purely distance to the natal river could be driving the distribution patterns.

The consistency of the presence of these two hotspots is consistent with other studies that show migration and distribution patterns being stable in time either for entire groups of Chinook salmon stocks (Larson *et al.*, 2013), for single stocks (Tucker *et al.*, 2012), single runs (Weitkamp, 2010), or for different groups of the same run (Norris *et al.*, 2000), although none of these studies documents stable distributions at the local scale. Findings of Satterthwaite *et al.* (2013) show, in contrast, a different picture when looking at individual runs and age groups of Central Valley. They found particularly for the Sacramento River fall-run age 3 distribution not only seasonal but also interannual variation, which they relate to changes in SST. The fixed migration pattern we found suggests a strong genetic component not only at broad (Kallio-Nyber and Ikonen, 1992; Quinn and Chamberlin, 2011) but also at intermediate spatial scales. However, when looking at very fine spatial scales, i.e. at the scale of our grid cells of $\sim$90 km^2, slight changes over time can be observed indicating dynamic external factors being similarly at play as suggested by Satterthwaite *et al.* (2013). Distributional patterns of Pacific Chinook salmon can be driven by various other components, such as geospatial variables (Yu *et al.*, 2012; Burke *et al.*, 2013), local and regional oceanic environmental conditions (Hare and Francis, 1995; Greene *et al.*, 2005; Wells *et al.*, 2006; Bi *et al.*, 2007; Fisher *et al.*, 2007; Pool *et al.*, 2012; Sharma *et al.*, 2013), and foraging (Peterson *et al.*, 2010; Bi *et al.*, 2011; Yu *et al.*, 2012). Also, the commercial salmon troll fishers from this region use temperature and ocean current edges to help them locate fish concentrations (pers. comm. with fishers) indicating that fine-scale ocean features influence distribution.

When linking Klamath catches and CPUE in this particular study region with bathymetric, geospatial, and SST as an environmental variable, we found a similar negative and saturating effect of the shore distance as Burke *et al.* (2013) found for two Columbia River stocks. Interestingly, shore distance only affects the probability of catching Klamath, not its density, which stands in contrast to

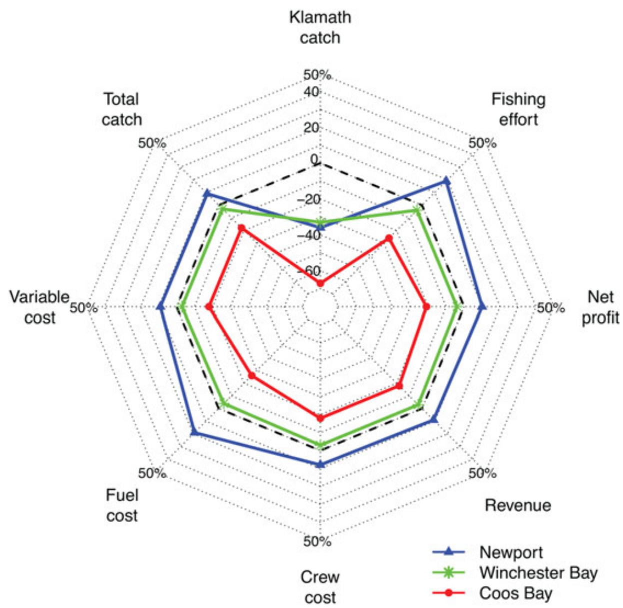

Figure 6. A radar chart illustrating the fleet-specific changes in total annual catch, effort, and economic parameters when adapting fishing allocations based on ScenConst (expressed in % change relative to ScenOpt). This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

findings of Burke *et al.* (2013). Only bathymetry affected both parameters. High slope and bottom depth are found at the continental shelf, where fish tend to aggregate. These variables would be expected to have more explanatory power than shore distance since the offshore distance to the shelf varies with latitude. Our model results indicate further that Klamath seems to aggregate or favour a depth of 120–150 m. Here, catch probabilities are highest with similarly high CPUE. This finding stands in contrast to various studies that found no depth effect on abundance (Bi *et al.*, 2007, 2011; Peterson *et al.*, 2010; Yu *et al.*, 2012). The insignificance of monthly mean SST at the scale of month and grid cell could suggest that SST is less suited as an indicator of hydrological conditions for Klamath than we initially assumed. Similarly, Sharma *et al.* (2013) could not detect an SST effect on Klamath survival rates. This could be because Klamath is generally found at greater depth and therefore SST does not have a direct effect. Yet fishers use SST as a cue to locate fish. This suggests that a finer-scale analysis (in both space and time) is needed to identify the relationship between surface ocean conditions and fish distributions. One component not included in this analysis was prey availability as fine-resolution data were unfortunately lacking. The relevance of bottom-up processes have been demonstrated through positive chlorophyll *a* as well as copepod effects on Chinook salmon in general (Peterson *et al.*, 2010) and it surely plays a crucial role for Klamath fish. This shows the opportunity for further progress in disentangling the key elements that drive stock-specific abundance and distribution to foresee impacts of climate change and incorporate these dynamics in bioeconomic modelling tools useful for stakeholders.

Does Klamath aggregate with other stocks in the ocean?

One study aim was to identify the stocks Klamath co-occurs with and to tackle the questions whether there is potential for fishers to avoid catch of Klamath and still catch other stocks. This is relevant from a fishers's economic perspective as well as from a management perspective when protecting other weak stocks. The results show that Klamath co-occurred strongly with several stocks. This spatial overlap pattern was temporally consistent supporting findings that stock-specific distributions do not vary greatly in time (e.g. Tucker *et al.*, 2012; Larson *et al.*, 2013). The greatest overlap occurred with northern California/southern Oregon coast, which confirms Weitkamps' study (2010) where she found similar broad-scale recovery patterns of tagged Chinook salmon that originated from the same freshwater region. In general, Klamath overlapped to varying degrees with all stocks that originated south of the Columbia River, except for Central Valley spring and winter run, which have a much more southerly distributional centre (Bellinger *et al.*, 2015). The generally observed spatial overlap between Klamath and California coast at broad scales (Satterthwaite *et al.*, 2014; Bellinger *et al.*, 2015) also occurs at fine spatial scales as shown in our analysis, which supports the use of Klamath as an indicator of fishing pressure for the California coast stock. The finding of Satterthwaite *et al.* (2014) that distributions of Klamath and California coast Chinook were similar early in the year, but diverged in late summer and fall, however, was only confirmed in Oregon for some years. Our analysis did not include the areas in California where late-season divergence was most pronounced.

Most of the stocks originating north of the Columbia River also had high *SOI* values. Although the northern stocks are known to migrate mainly farther north (Tucker *et al.*, 2012), they also have a much wider distributional range (Weitkamp, 2010), and some individuals seem to migrate for some period slightly south. The co-occurrence values were in fact observed for stocks that originated from the Columbia River basin. All these stocks had, within our study region, a distributional centre that was farther northeast of Klamath (except for mid-upper Columbia spring). These stocks are known to undertake a rapid northward migration to Alaskan waters (Trudel, 2009; Tucker *et al.*, 2011), with large numbers (93%) caught north of the Columbia River mouth (Wahle *et al.*, 1981). This suggests that fishing outside of the Klamath hotspots seems to be a possible strategy and could lead, in the north, to potentially higher catch of Columbia River stocks. Current fishery management practices take advantage of this distributional pattern, although at a coarser scale. Here, it must be emphasized to note that some of these stocks, i.e. Willamette, Snake fall, and lower Columbia River, are also listed as threatened under the ESA (Federal Register, 2015) with no recovering trend in the recent past (NMFS, 2015b). Changes in fishing allocation might have implications for these stocks, but as their overall catch in this region is generally low, impacts may be minimal. However, NMFS places strict constraints on fishing impacts on these stocks, and actions to limit Klamath catch could increase Columbia and Snake River stock impacts above conservation limits. Fishing outside of the Klamath hotspot in the south might lead to higher catch of the Central Valley fall stock, which has a more southern distributional centre. The status of this stock has been highly variable over the past decade, with record high and low abundance. The other potential strategy of fishing outside the main Klamath depth range at certain times to avoid its catch proved to be less suitable since almost all overlapping stocks show a similar depth distribution.

Possibilities of fishing adaptation to reduce bycatch

Statistical modelling indicated that catch of Klamath might be reduced by shifting effort to other locations, outside the hotspots.

However, it still remains open to what extent catch could be reduced and whether changes in fleet behaviour could be economically favourable. Incorporating these findings into a spatially explicit bioeconomic model demonstrated that effort allocation adaptations could be a useful strategy to reduce overall Klamath catch, in our ScenConst by up to 30%. At the same time, the model simulation, when maximizing net profits for all fleets, showed the potential for some fleets to maintain or even increase profits. But that largely depends on distance from the home port to new fishing locations. Allocation of fishing effort is largely determined by distribution of the target fish species, to allow for high catch rates (Hilborn and Ledbetter, 1979). However, it also reflects regulatory and economic constraints (Botsford *et al.*, 2009) with higher effort in areas where fishing costs (e.g. fuel costs) are lower. This is the reason effort allocation is often related to distance from home ports (Sampson, 1991; Caddy and Carocci, 1999). In this model, the Coos Bay fleet is an example where distances to the newly allocated fishing grounds are greater and hence fishing can become more cost-intensive, with fuel costs, which are also regarded as main drivers by local fishers (pers. comm.), driving net profits down. On the other hand, displacing effort closer to the harbour compared with a more productive offshore region is a trade-off between fuel savings and fishing efficiency in which savings in fuel costs are sometimes adequate to compensate for the loss in landing value (Simons *et al.*, 2014b) and sometimes not (Bastardie *et al.*, 2010). For Newport, the trade-off between lower fuel costs and higher fishing effort in the near-port area that is relatively Klamath-free seems to be overall economically beneficial for the fleet.

The idea of fishers responding to economic incentives with effort allocation is supported by several studies (Bockstael and Opaluch, 1983; Dorn, 1998, Simons *et al.*, 2014b). For example, Bockstael and Opaluch (1983) provide empirical documentation showing that fishers adjust their effort in response to changes. In our model, fleets are assumed to respond to profits of the whole fishery. Modelled species profitability, catch rates, Klamath limits, and fishing costs consequently influence not only the spatio-temporal distribution of fishing effort but also the overall effort level and profit. In addition to fine-scale effort shifts, the model output suggests an overall shift in effort from Coos Bay, closest to the Klamath hotspots, to Newport, closer to an area where Klamath was generally caught at lower rates in the four years studied. Thus, predicted total catch and, consequently, net profit decrease for Coos Bay and increase for Newport. In summary, adaptation in effort allocation can serve both species conservation and economic interests. For the latter, however, single fishers or fleets may be negatively affected, while a group of fishers or fleets generally benefits. Therefore, in addition to stock-specific area quotas, targeted closures, or other policy approaches, reallocating fishing effort between fleets or temporally changing the landing port could be a new management strategy to consider.

Model improvements and application to management

The model built in this study represents a simplified version of the more complex recent models (Salz *et al.*, 2011; Simons *et al.*, 2014a), as the main interest here was to develop a tool that is easy to understand and can be used strategically to explore the general potential of fishing adaptations and their implications to rebuild a weak stock. The bioeconomic model at its present stage does not allow for quantitative conclusions, as it does not include biological processes (e.g. stock–recruitment or demographic processes), stochasticity to reflect natural variability, or economic components such as risk factors for "search" effort, behaviour switching between fisheries, and fleet communication. The assumption of simple logistic growth further does not reflect the biology of Chinook salmon and, hence, might have led to over- or underestimation of calculated stock size, but it was the best solution at this stage. The assumption of 25 vessels for each fleet is a realistic approximation of the number of vessels sampled in three of the four ports. It was a great overestimation for Garibaldi as the annual sea-days were just ~27. This might explain why model results showed no differences under the two model scenarios vs. the observed pattern during our study period. Indeed, model performance would benefit from more realistic vessel numbers, as this will affect the estimation of the fleet's net profit, which is the main driver for the effort allocation CONOPT algorithm. On the other hand, this model result could have been caused by the undersampled fishing effort of the fleet. It is likely that fishers from Garibaldi sometimes fish farther south, where densities of Chinook salmon and Klamath are higher. If so, this would likely have caused an effort allocation change under the profit-optimization and the constrained Klamath harvest scenario. However, we believe that the model outcomes of the other three fleets are not greatly impacted by the overestimation of vessels for the Garibaldi fleet.

The data on which the bioeconomic model and statistical analysis are built is a comprehensive and unique collection with high spatio-temporal resolution allowing for such fine-scale study. But, it still represents only a 15% sample of the entire fishery, and the sample distribution was influenced by the sampling design. In general, commercial fishing data, which are influenced by fishing fleet efficiency and behaviour, are often regarded as less suitable for estimating stock abundance. Although Bellinger *et al.* (2015) have recently tested for potential biases of individual fishers on CPUE-based abundance estimates in this fishery and found limited effects, additional survey data could shed more light on individual stock distributions. Fishers stated that they might miss temporary hotspots and consequently identified stock distribution might not fully reflect the real pattern. To be able to identify trends and periodic patterns in stock distribution with more confidence, a longer time-series is needed, along with a sampling programme designed to more uniformly represent the fishery.

In addition, the modelling reported here was based on aggregated monthly fish distributions over 4 years of sampling. Fish distributions change from year-to-year, and a strategy based on averages will not always be useful. For example, in the Newport area, catch rates were sometimes high nearshore and at other times high offshore, so a nearshore fishing strategy would not be cost-effective at all times. One possible solution would be to assess stock distributions in near real time and identify areas with both high catch rates and lower Klamath contribution rates, then encourage the fleet to fish those areas. Using an Internet-based fishery information system, spatial and electronic data entry at sea, catch, and effort data can be available as soon as a fishers returns to port and gains an Internet connection. Stock identifications can be attached to individual fish within 2 days of samples arriving at the genetics lab. Realistically, stock-specific distributions can be available to fishers in a format suitable for decision-making within a week of fish being caught. Particularly as changes in fishing allocations could lead to increased catch of other weak stocks, as suggested in our analysis, it must be emphasized to incorporate *ad hoc* adaptations of management strategies if other weak stocks show strong declines. Such model simulations could be then made available for stakeholders through a multi-user website, such as the Internet platform FishTrax (www.pacificfishtrax.org). This platform aims to bridge the gap between academia, fishery management agencies, and the industry and provides access to various portals and databases. An improved version of the presented bioeconomic model could be integrated in such a web portal to allow fishers to adapt their economic parameters and create scenarios to predict suitable changes in individual and fleet behaviour. The feasibility of collecting such fine-scale data to support FishTrax and other similar systems certainly represents a persistent challenge, but with continual advancements in technological capabilities, the cost of gathering and processing these data make it ever more realistic.

Transdisciplinary challenges and chances

In this study, human and natural science disciplines were combined to provide new insights into potential future strategies both beneficial for the fishing sector and Chinook salmon conservation. The patterns and strategies that emerged from this research were not only the result of combining multiple disciplines but also the participation of the fishing sector. Collaboration with stakeholders from the start is a crucial step in advancing sustainable fishery research and one of the key points that makes a TD approach more holistic than other disciplinary strategies (Stock and Burton, 2011). While collaborations among researchers and between researchers and practitioners is pivotal when finding solutions for real-world problems, they also bear great challenges. For example, the heterogeneous nature of collaborators often leads to access to a wider range of knowledge. This can be beneficial, but at the same time, it can also create opportunities for disagreement and conflicts (Hoffmann-Riem *et al.*, 2008). Another major issue is communication that requires translatability since the TD project team consists of researchers trained in different scientific fields with their own philosophies and terminologies. Similarly, non-academic stakeholders have their own language. Finding a common baseline vocabulary is consequently key to construct an integrated framework, but not easy to achieve (Holbrook, 2013). One way to facilitate TD is thus to establish a communication framework across disparate disciplines and stakeholders. Here, modern information systems become increasingly important as they enable communication and knowledge sharing across broad social and cultural boundaries.

Conclusion

Bringing together disciplines from the human and natural sciences and stakeholder participation enabled us to analyse a complex and multidimensional socio-ecological system in ways that provided real-world insights that are not attainable with lower-dimension analysis. By using this transdisciplinary approach, we showed a potential strategy of bycatch avoidance in the Chinook salmon ocean fishery. First, we identified the fine-scale distribution and hotspots of the indicator stock Klamath and the role of bathymetry. We then identified Klamath associations with other stocks and evaluated the potential implications for non-overlapping, weak stocks if the fishing effort shifts away from these Klamath hot zones. Scenarios from a simplified bioeconomic model demonstrate that such effort reallocation could lead to reduction in Klamath catch, but also to increases in net profit depending on the distance of the fleets' home port. The output of the model at its current stage should be regarded rather strategically, providing a qualitative understanding of how individual fleets can be affected differently and of the types of best fleet strategies. While enforcement of regulations can be costly at times, incentive structures for self-regulation could be an alternative to consider for management plans. Despite some challenges in TD research and despite the present limitations to incorporating fine-scale changes in Chinook salmon stock distributions in management regulations, this direction will become increasingly attractive for use in fishery management.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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