Recruitment signals in juvenile cod surveys depend on thermal growth conditions

Benjamin J. Laurel, David Cote, Robert S. Gregory, Lauren Rogers, Halvor Knutsen, and Esben Moland Olsen

Abstract: Coastal seine surveys contain some of the only direct measures of age-0 abundance for Atlantic cod (*Gadus morhua*) and Pacific cod (*Gadus macrocephalus*), yet their utility in forecasting future year-class strength has not been evaluated among regions. We analyzed coastal time series from the Gulf of Alaska, Newfoundland, and Norway to test the hypothesis that recruitment signals are stronger when assessed under thermal conditions that provide high juvenile growth potential. Weaker recruitment signals were associated with low growth potential from cold winters (Newfoundland) and recent warmer summers (Norway). We conclude that temperature-dependent growth strongly influences the utility of coastal surveys in recruitment forecasting among regions. Temporal changes in growth potential (e.g., via climate change) will likely affect recruitment signals by way of changes in juvenile mortality or spatial shifts to more favorable thermal habitats.

Résumé : Si les relevés côtiers à la senne constituent un des rares moyens d'obtenir des mesures directes de l'abondance de la classe d'âge 0 pour la morue franche (*Gadus morhua*) et la morue du Pacifique (*Gadus macrocephalus*), leur utilité pour prédire la force future des classes d'âge n'a pas été évaluée entre différentes régions. Nous avons analysé des séries chronologiques côtières pour le golfe de l'Alaska, Terre-Neuve et la Norvège afin de vérifier l'hypothèse selon laquelle les signaux de recrutement sont plus forts quand ils sont évalués pour des conditions thermiques qui assurent aux juvéniles un potentiel de croissance élevé. Des signaux de recrutement plus faibles étaient associés à un faible potentiel de croissance découlant d'hivers froids (Terre-Neuve) et d'étés plus chauds récents (Norvège). Nous en concluons que la croissance dépendante de la température a une forte incidence sur l'utilité des relevés côtiers pour prédire le recrutement entre régions. Des variations temporelles du potentiel de croissance (p. ex., découlant de changements climatiques) auront vraisemblablement une incidence sur les signaux de recrutement, par l'entremise de modifications de la mortalité des juvéniles ou de déplacements dans l'espace vers des niches thermiques plus favorables. [Traduit par la Rédaction]

Introduction

Marine teleost fishes of the Family Gadidae comprise some the largest and most valuable wild fisheries in the world (e.g., Atlantic cod, *Gadus morhua*; walleye pollock, *Gadus chalcogrammus*) and are characterized by high fecundity and high spatiotemporal variability in year-class survival and subsequent recruitment to adult populations. In spite of extensive population sizes, gadid stocks are vulnerable to overfishing and sensitive to environmental variability when not managed carefully and adaptively in response to year-to-year variation in recruitment success (Taggart et al. 1994; Cushing 1995). Consequently, prerecruit stages may be assessed to anticipate future harvest quotas, evaluate alternative management actions, and prepare for socioeconomic consequences of "recruitment failure" (Hutchings and Myers 1994; MacKenzie et al. 2008). However, recruitment prediction in marine gadids has remained challenging despite greater than a century of devoted fisheries science (Hjort 1914; Houde 2008).

Forecasting recruitment from early life stages (e.g., eggs and larvae) is complicated by multiple factors, many of which are attributed to unaccounted sources of mortality prior to settlement (Sissenwine 1984; Bailey and Houde 1989). Eggs and larvae are highly vulnerable to stochastic processes (e.g., advection, prey fields, temperature) because they lack the energetic reserves and swimming ability of older life stages. As such, cohorts of marine fish larvae can "disappear" within days after a survey if the prey field changes or predators are numerous (Paradis et al. 1996). It logically follows that surveys made closer in time to when recruitment to the fishery occurs (e.g., juvenile surveys) should be more accurate than surveys conducted at earlier life stages (eggs and larvae; Stige et al. 2013), and this has led attention to the use of age-0 juvenile abundance data to forecast recruitment in dynamic marine systems (Sissenwine 1984; Houde 1987; Peterman et al. 1988).

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Forecasting recruitment from age-0 stages in gadid fisheries has been complicated by factors that stem principally from the spatial separation of juveniles and adults. Fishery-independent trawl surveys are typically conducted in offshore regions, yet juveniles are often most abundant in shallow, coastal nursery areas where environmental conditions (e.g., temperature, macrophytes, and food) are optimal for rapid growth and predator refugia are accessible to them (Gotceitas et al. 1997; Fromentin et al. 2001; Linehan et al. 2001; Laurel et al. 2003a). Although trawl survey gear may occasionally capture age-0 juvenile fish, estimates of small juveniles tend to be biased because of gear selectivity (Methven and Schneider 1998; Williams et al. 2011) or the changes in seabed habitat associations in their early life (Fraser et al. 1996; Gregory and Anderson 1997). Pelagic age-0 surveys may also be prone to high measurement error if they are conducted across the settlement period (Mukhina et al. 2003). Therefore, offshore estimates of earlier pelagic stages may be poorer predictors of recruitment relative to postsettled juveniles (Helle et al. 2000; Stige et al. 2013; Ohlberger et al. 2014).

Demersal beach seine surveys sample juveniles after settlement in nursery habitats and provide the only reliable measures of age-0 and age-1 abundance of commercially important gadids in some ecosystems (Tveite 1984; Ings et al. 1997). Seine surveys typically collect postsettled age-0 gadids in 2–4 m of water during late summer – early fall (Ings et al. 1997; Laurel et al. 2003b) at densities several orders of magnitude higher than those reported offshore (Dannevig 1933; Bulatova 1962; Dalley and Anderson 1997; Hurst et al. 2015). Indeed, older juvenile stages of gadids (ages 1–2) often remain in shallow coastal waters before moving into deeper water away from shore as adults (Dalley and Anderson 1997; Stenseth et al. 1999; Cote et al. 2004; Laurel et al. 2009); therefore, they may be available to nearshore sampling gear. However, seine surveys potentially offer an early window into future health of gadid populations, are relatively cost-effective, and often contain some of the only direct measures of age-0 abundance for some gadid populations.

Prior attempts at establishing recruitment links in age-0 gadids from seine surveys have yielded mixed results within and across systems. In Norway, where juvenile coastal Skagerrak cod has been monitored since 1919, multiple studies have detected recruitment signals between age-0 and age-1 year classes (e.g., Fromentin et al. 2001) and between age-0 and older age classes (e.g., Tveite 1992). In Newfoundland, recruitment signals using age-0 cod appear to be relatively weak or observable only on a rank order basis (Ings et al. 1997), although signals using age-1 cod have shown much more promise (Gregory et al. 2006). Differences in recruitment signals within and among regions suggest that postsettlement mortality can be significant in coastal nurseries and that year-class strength is not necessarily established at the "age-0" stage. However, analyses of seine surveys from regions outside of Norway have been based on relatively short time series.

Postsettlement mortality in juvenile fish is largely determined by size-dependent processes driven by predation (e.g., Sogard 1997). Therefore, it is a commonly held viewpoint that accelerated growth through these early life stages results in decreased predation exposure and an increased likelihood of survival to adulthood (Miller et al. 1988; Houde 2008). Temperature is arguably the most important environmental component driving growth in marine fish, which is secondarily modified by food availability (Jobling 1988). High-growth environments also allow juvenile gadids to store sufficient lipid reserves to survive their first overwintering period (Copeman et al. 2008, Heintz et al. 2013). This is especially important in subarctic and Arctic regions where the summer growth period may be short and winter is harsh and prolonged (<0 °C for >3 months; Bouchard and Fortier 2011). Therefore, the thermal growth response of fish provides some indication of survival likelihood in the first year of life under varying temperature regimes (Anderson 1988).

In this study, we examined whether, and under what conditions, coastal seine surveys for postsettled juvenile gadids provide a strong age-0 signal for forecasting year-class strength of older ages (henceforth referred to as "recruitment signals"). Our approach was to conduct a within- and among-region comparison of recruitment signals using time series from southeastern Norway (Skagerrak Coast), the Northeast Newfoundland Shelf (Bonavista Bay), and Gulf of Alaska (Kodiak Island). We selected these coastal regions because they (i) have associated time-series data on age-0 and age-1 gadid life stages and (ii) reflect the broad marine environmental characteristics of "Sub-Arctic" (northeastern Newfoundland) "North Temperate" (southeastern Norway), and "Boreal" (Gulf of Alaska) ecosystems. Using each regional time series, we tested the hypothesis that recruitment signals are positively linked to temperature-dependent growth potential. Our overall goal was to evaluate the utility of coastal seine surveys in regional cod assessments and determine whether changes in climate-regulated growth have the potential to enhance or deteriorate recruitment signals within these regions.

Methods

Age-0 and age-1 surveys

We restricted our analysis to seine hauls at fixed-site locations and standardized sampling periods across regions (Fig. 1). Summary descriptions of each regional time series are listed in Table 1, and temporal changes in catch abundance are illustrated in Fig. 2. An expanded description of sampling details and focal species for each region is provided below.

Norway, Skagerrak coast (G. morhua)

Coastal cod populations inhabit fjords and other nearshore areas along the Norwegian Skagerrak coast. Spawning occurs in January–April and typically peaks in February–March (Espeland et al. 2007; Ciannelli et al. 2010). Juveniles settle into nearshore demersal habitats in May–June, where they remain for at least a year (Dahl and Dannevig 1906). The nursery habitats consist of eelgrass (Zostera marina), various macroalgae species such as the serrated wrack (Fucus serratus), and nonvegetated soft-bottom areas, where the percentage of floral cover appears to have increased during recent decades (Barceló et al. 2016). Skagerrak coastal cod from interior fjord regions are genetically distinct from offshore North Sea cod populations, although there is evidence that North Sea cod larvae drift into nearshore areas (Stenseth et al. 2006) and potentially use them as nurseries (Knutsen et al. 2011). Mechanisms for maintaining local population structure in Skagerrak coastal cod likely involve spawning in sheltered fjord basins, where eggs and larvae are protected from coastal currents combined with limited movement of older juveniles (Knutsen et al. 2007; Ciannelli et al. 2010; Rogers et al. 2014). Often, cod in this region will maintain restricted nearshore home ranges through the mature life stage, although these older fish typically inhabit deeper habitats compared with juveniles (Aalvik et al. 2015). Skagerrak coastal cod typically have short life histories, growing 10–15 cm per year and maturing at an age of 2–4 years and 30–50 cm (Olsen et al. 2004). The Flødevigen beach seine survey began in 1919 and continues today with the intent of monitoring annual changes in the recruitment signals of Atlantic cod (see Stenseth et al. 1999). The seine was 38 m long and 3.8 m deep with a stretched mesh size of 15 mm. The seine was deployed from shore by a small boat and hauled by two people standing on shore. Every autumn (September–October), the seine was hauled at >100 fixed sites along the Norwegian Skagerrak coast (Fig. 1), targeting age-0 cod, but also capturing age-1 and older cod and other species. Maximum depth of the seine sites ranged from 3 to 15 m with a total sampled area up to 700 m² per site. All cod were counted and total length (TL) was measured to the nearest centimetre. Ages were determined based on a mixture analysis applied

Fig. 1. Map showing regions of comparison (squares, top panel). Subpanels provide a view of each region, with circle(s) representing fjord or embayments containing 8–18 fixed-site locations where seines were deployed seasonally and (or) annually. See Table 1 for details.

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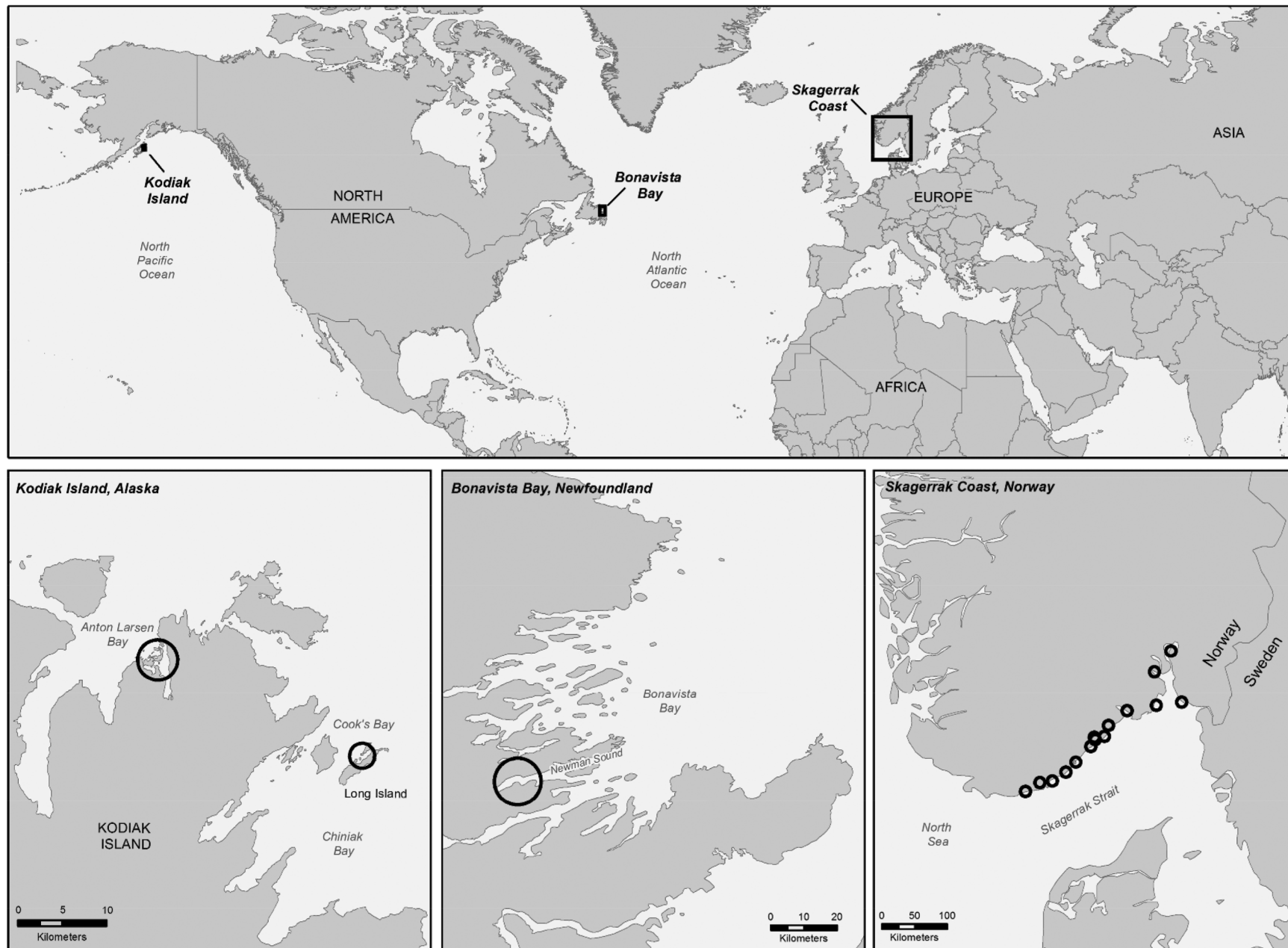
Can. J. Fish. Aquat. Sci. Vol. 74, 2017

Table 1. Summary of regional time series using demersal beach seines to capture juvenile cod species (*Gadus morhua* and *Gadus macrocephalus*).

Region	Time series	Swept area of seine (m²)	No. of sites	Sampling months	Sampling frequency (hauls per site per year)	Gadid(s) targeted	Size at age 0 (mm SL)[a]	Size at age 1 (mm SL)[a]
Norway (Skagerrak coast)	1919–2011	700	109	Sept.–Oct.	1	*G. morhua*	50–150	203–271
Newfoundland (Newman Sound)	1996–2014	880	12	July–Dec.	10	*G. morhua*	25–115	121–149
						G. macrocephalus	45–120	146–172
Alaska (Kodiak Island)	2006–2013	900	16	July–Aug.	4	*G. macrocephalus*	35–120	160–229

[a]Fish sizes for Alaska and Newfoundland regions are based on late August–September sampling portions of the survey only.

to length–frequency distributions for each year and region (details in Rogers et al. 2011). Sampling sites were grouped into 15 regions, ranging from the southern tip of Norway northward to Oslo Fjord and eastward to the Swedish border. We used survey data from 1919 to 2011 for our analyses (93 years). Because some stations were discontinued and others were occasionally added, we only analyzed data from stations sampled 40 years or greater (*n* = 109 stations). Each region contained 2–13 sampling stations. Samples from over 15 000 seine hauls comprised the data available for analysis. Temperatures were recorded in the bay at a single location near Flødevigen Research Station at 1 m on a near-daily basis since 1919.

Newfoundland, Newman Sound (G. morhua *and* Gadus macrocephalus ogac)

In the summer and fall, age-0 and age-1 juvenile *G. morhua* and *G. macrocephalus ogac* are common in the nearshore coastal waters of Newfoundland (Gotceitas et al. 1997; Laurel et al. 2003*b*; Gregory et al. 2006). The Northwest Atlantic population of Atlantic cod (the "northern cod stock"), off northeastern Newfoundland, historically ranged over most of the continental shelf from shallow coastal waters to the edge of the continental slope (Templeman 1979). However, young juveniles (ages 0–1) of this population are predominantly distributed in coastal waters until at least age 2 (Bulatova 1962; Dalley and Anderson 1997). In contrast, Greenland cod are predominantly coastal throughout their life (Scott and Scott 1988). Recent molecular evidence has indicated that Greenland cod is actually a subspecies of Pacific cod (*G. macrocephalus*; Carr et al. 1999); henceforth, we use *G. macrocephalus* for both Greenland cod (in Newfoundland) and Pacific cod (in Alaska), but refer to the common name to distinguish the region of capture.

Spawning by Atlantic cod in Newfoundland peaks in May, but is generally protracted throughout the summer (Rideout and Rose 2006). Age-0 juveniles settle from the pelagia in several distinct recruitment pulses through summer and autumn each year (Methven and Bajdik 1994; Ings et al. 2008). Timing of these recruitment pulses is associated with favorable combinations of episodic upwelling, following strong southwest winds (Ings et al. 2008), coastal currents (deYoung and Rose 1993), and local wind-driven surface dispersal (Stanley et al. 2012).

In contrast with Atlantic cod, the early life history of Greenland cod is poorly understood. Spawning appears to be coastal and is known to occur under ice in the early spring — in March and April (Scott and Scott 1988). Age-0 juveniles settle in a single recruitment pulse in July or early August (Ings et al. 2008), cohabiting the coastal zone with Atlantic cod throughout their first years of demersal life (Laurel et al. 2003*b*; Ings et al. 2008).

Over an 18-year period (1996–2014), abundance of age-0 and age-1 demersal juvenile Atlantic and Greenland cod was determined every 2 weeks from July to November (10–11 sample periods annually), at each of 12 sites in Newman Sound, Newfoundland, Canada (Fig. 1; Table 1); data from a total of 1680 seine hauls were available for analysis. Nearshore substrate varied between complex eelgrass-mixed mud–pebble habitats to nonvegetated sand–pebble–cobble habitat.

A 25 m long × 2 m high Danish bag seine net (9 mm mesh in the cod end) was used for collections. The net was deployed from shore using a small boat to a distance of 55 m, at a typical depth of 5–6 m. The seine was hauled ashore by two people standing 16 m apart. The net sampled from the seabed to 2 m above bottom and, as deployed, sampled an area of 880 m² of the seabed. Escapement rate of juvenile cod in the seine path is typically low (<5%; Gotceitas et al. 1997). Captured fish were then identified, counted, and measured to standard length (mm SL) before being returned alive to their site of capture. Juvenile cod were assigned to tentative age groups based on previously established age–length relationships in Newfoundland waters in late autumn (Dalley and Anderson 1997) and confirmed for age-0 and age-1 fish by annual length–frequency trajectories and otolith microstructure.

Water temperatures were monitored (Hugrun 1998–2001, Vemco Mini-T, 2002–14 thermographs) at four locations 50 cm above the seabed in approximately 3 m depth. Water temperatures were recorded throughout the year every 4 h (1998–2001) or hourly (2002–2014). Seasonally, temperatures in the nearshore ranged from 20 °C in late August to –1.0 °C in early December and through winter, rising again in late April or May. Daily temperatures vary little (±1.0 °C) among the four locations.

### Alaska, Kodiak Island (G. macrocephalus)

Age-0 and age-1 juvenile *G. macrocephalus* inhabit embayments around Kodiak Island and can be collected by beach seine between early July and October (Abookire et al. 2007; Laurel et al. 2007). Older juveniles move to deeper water, but are still found locally (<20 m depth) throughout the summer and fall (Laurel et al. 2009). Densities of age-0 juveniles are highest in shallow, vegetated habitats (*Laminaria* spp. and *Zostera* spp.) during settlement in July, but then expand into a broader range of habitats in late August (Laurel et al. 2007).

The beach seine survey for age-0 and age-1 *G. macrocephalus* occurs at 16 sites spread evenly across two embayments (Anton Larsen Bay (ALB) and "Cook Bay" (CB); Fig. 1). Maximum depth varies between 2 and 4 m among seine sites, and sites predominantly consisted of eelgrass *Zostera marina*, *Laminaria saccharina*, or "bare" mineral substrates (sand–small cobble). A total of six *Laminaria* (ALB: *n* = 3; CB: *n* = 3), six eelgrass (ALB: *n* = 3; CB: *n* = 3), and four bare (ALB: *n* = 2; CB: *n* = 2) fixed-site locations comprise the survey. Sites are surveyed twice on successive days during two separate time periods, 14–21 July and 21–28 August, in each year. A total of 8 years (2006–2013) were available for this study consisting of 512 seine hauls.

Sites were sampled using a 36 m demersal beach seine deployed from a boat and pulled to shore by two people standing a fixed distance apart on shore (see details in Laurel et al. 2007). The seine wings (13 mm mesh) were 1 m deep at the ends expanding to 2.25 m in the middle with 5 mm delta mesh in a bag-end. Juvenile *G. macrocephalus* from each seine haul were counted and measured (mm TL). Age-0 and age-1 individuals were differentiated by two distinct length groups, 35–120 and 160–220 mm TL, respectively.

Temperature data was provided by the Trident Basin record. The temperature record consisted of data from a single logging station located between Cook's Bay and Anton Larsen Bay (Fig. 1) at 10.7 m depth recording continuously all year.

Fig. 2. Interannual variability in age-0 and age-1 catch of *Gadus morhua* and *Gadus macrocephalus* by region. Catch per unit effort (CPUE) for each age class and region was mean-centered by subtracting the mean and dividing by the standard deviation using the "scale" function in R. Data details are available in Table 1.
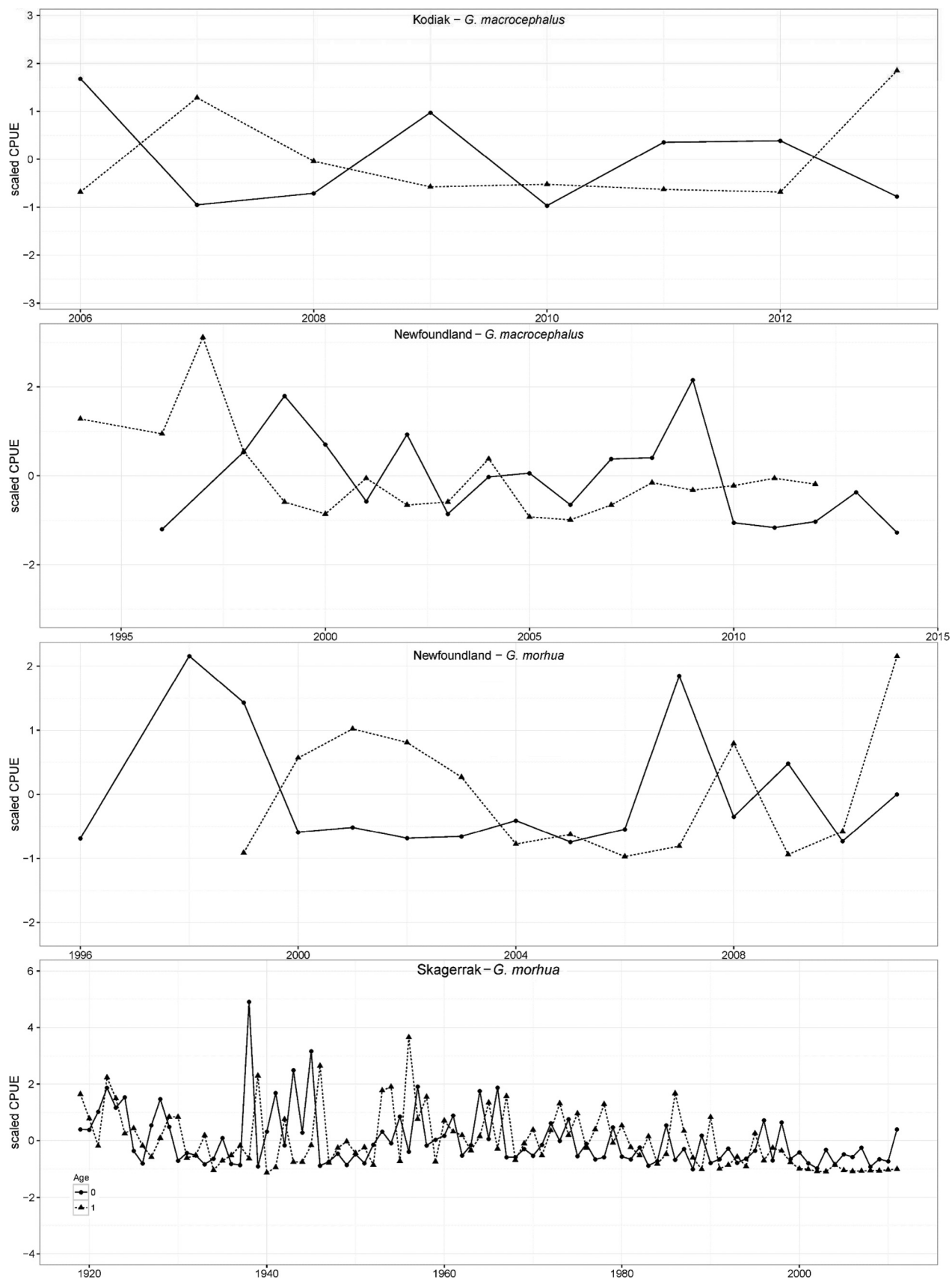
Age-2+ surveys

Age-2+ fish were variably surveyed across regions, but provide a relative index of abundance to compare with fixed-site, age-0, and age-1 beach seine surveys. In Norway, fishery recruitment was measured as the number of age-2 cod in the stock assessment for North Sea cod (ICES 2012). Although the North Sea stock is distinct from coastal populations, recruitment signals in the offshore stock may be detected in the coastal surveys owing to nursery habitat overlap and shared environmental influences on early-life stage survival. In Newfoundland, age-2 *G. morhua* occupy deeper coastal water (Bulatova 1962; Dalley and Anderson 1997) and are ineffectively sampled by beach seine and offshore research vessel surveys. However, the abundance of age-3 and older *G. morhua* in Newfoundland have been annually assessed as part of Canada's NAFO Division 2J3KL (i.e., northern cod) stock status reports (e.g., DFO 2013) since the late 1970s. For this study, age-3 fish assessments of *G. morhua* were used from an inshore bottom-trawl survey during July–August in NAFO statistical area 2J3KL (DFO 2013). Predictions of recruitment strength were not available for *G. macrocephalus* in Newfoundland, as stocks of this species are not commercially harvested or assessed. In Alaska, offshore trawl surveys capture age-2 fish, but assessments are conducted in alternate years, thereby providing only 4 years for analysis. However, coastal surveys of age-2 *G. macrocephalus* are available from an annual camera survey in the same region of the age-0 seine surveys (see details in Laurel et al. 2007; Stoner et al. 2008).

Approach and data analyses

Recruitment signal strength

We assessed the utility of coastal age-0 surveys to predict future year-class strength across a spectrum of corresponding age classes in future months and years that spanned older age-0 through to recruitment to the fishery (ages 2 and 3) in each region. While a deteriorating pattern of prediction strength was expected, the shape of that pattern was not known a priori. The occurrence of both *G. morhua* (Newfoundland and Norway) and *G. macrocephalus* (Newfoundland and Alaska) in two study areas for each species also allowed qualitative comparison of patterns among regions where environmental conditions or species ecology varied.

We assessed the predictive utility of a given age class using the following linear model:

$$\mathrm{Cod}_{t2} = a + \beta \times \mathrm{Cod}_{t1}$$

where Cod_{t1} is the (log-transformed) initial abundance of the target species and Cod_{t2} is the (log-transformed) abundance observed for that same year class at later dates. The strength of the relationship of multiple year classes ($n_{\mathrm{Newfoundland\text{-}Age\,0}} = 16$, $n_{\mathrm{Newfoundland\text{-}Age\,1}} = 13$, $n_{\mathrm{Newfoundland\text{-}Age\,3}} = 6$; $n_{\mathrm{Norway}} = 48$ to 92; $n_{\mathrm{Alaska\text{-}Age\,0}} = 8$, $n_{\mathrm{Alaska\text{-}Age\,1}} = 8$, $n_{\mathrm{Alaska\text{-}Age\,2}} = 7$) was estimated using the coefficient of determination (R^2) of the linear model. Though each region had significant linear models at alpha = 0.05, the percentage of significant results were heavily biased to Norwegian relationships (>80%) because of that region's extended time series and resulting statistical power. Such biases prevented p values from being used in comparisons across regions. The model intercept (α) and slope (β) were also not considered any further in the analysis.

To determine recruitment signal deterioration, the model compared initial abundance of age-0 cod (hereinafter referred to as "early") with age-0 abundance several months later in each year (hereinafter referred to as "late"). These model runs were restricted to Alaska and Newfoundland where multiple site visits were conducted each year. Comparisons of abundance of early age-0 to age-1 cod were conducted in all study areas, whereas comparisons with the abundance of age classes older than age-1 year were only included in Alaska (age 2 — camera survey) and Newfoundland (age 3 — inshore stratified surveys). Owing to rep-

lication of sampling in time (Newfoundland) and space (all sites), abundance was averaged for each month, year, and age class. In Norway and Alaska, where sampling areas were widely separated, model runs were compiled separately for each bay or fjord and then averaged. The relationship between age and utility for predicting future recruitment strength was similarly assessed except that the age class used for prediction varied and the predicted age class was static (when individuals were recruited (Newfoundland and Norway) or nearly recruited (Alaska) to the commercial fishery). Fishery recruitment was measured with the inshore mobile survey (Newfoundland) or camera survey (Alaska) and taken from the North Sea cod stock assessment, which is partly based on offshore trawl surveys (Norway).

Modeling regional growth potential

Daily growth potential was modeled for each region using available seabed temperature data and laboratory-measured temperature-dependent growth models of age-0 juvenile gadids (1–10 g individuals) for each species (Fig. 3). Growth models for Pacific and Greenland cod were based on experiments of *G. macrocephalus* collected in Gulf of Alaska (Laurel et al. 2016) and for Atlantic cod using *G. morhua* sourced from Norway (Björnsson et al. 2001). Although these models do not account for possible population-specific growth parameters in cod (Hutchings et al. 2007), temperature-dependent growth potential varies significantly among species of similar size within north temperate to subarctic regions (Otterlei et al. 1999; Björnsson et al. 2001; Imsland et al. 2005; Laurel et al. 2016). The growth models indicate both species can grow across a broad range of temperatures, but *G. macrocephalus* has comparatively higher growth potential at cold temperatures, whereas *G. morhua* has higher growth potential at warmer temperatures (Fig. 3).

Daily growth potential was plotted for each region using the two most recent decades (1995–2014) of available temperature data. Data were visualized in comparisons of same species in separate regions (*G. morhua*: Norway versus Newfoundland; *G. macrocephalus*: Newfoundland versus Kodiak Island). Growth potential data were then averaged across the summer and winter period for each year and analyzed by two-way analysis of variance (ANOVA) to determine if growth potential was statistically different by region and season for each species. An additional analysis was conducted to determine how growth potential changes within a region impacts the strength of recruitment signals through time. This analysis was conducted for the longest time series (Norway) where surveys have spanned across regional climatic changes (Rogers et al. 2011). We calculated Pearson correlations over a moving 10-year window between (log-transformed) age-0 and age-1 abundances in the coastal survey to assess the strength of the relationship through time. This window was compared with a moving average of the summer growth potential, calculated as described above. Abrupt changes in growth potential were examined by STARS (sequential t test analysis of regime shifts; Rodionov 2004), a software program written in Visual Basic for Application (Excel). The STARS statistic was used to detect a break-point in the summer growth potential time series, and the strength of the recruitment signal before and after this break-point was compared. For STARS analysis, we set $\alpha = 0.05$; the length of the proposed growth regimes (L) was set to 10 years to match the moving 10-year window of the age-0 and age-1 abundance correlation.

Results

Recruitment signals

The strength of recruitment signals declined as the time between indices increased and varied both by region and by species (Fig. 4). As expected, relationships were the strongest when comparing indices measured closest in time (e.g., between early and

Fig. 3. Temperature-dependent age-0 growth models for the two focal cod species: Atlantic cod (*Gadus morhua*) and Pacific–Greenland cod (*Gadus macrocephalus*). Each model predicts growth (*G*, % wet mass·day^{-1}) at a maximum food ration under laboratory conditions (see Björnsson et al. 2001 and Laurel et al. 2015 for details). Models were applied to daily temperature records from the past 15 years to determine maximum seasonal growth potential in each region (Figs. 6 and 7).
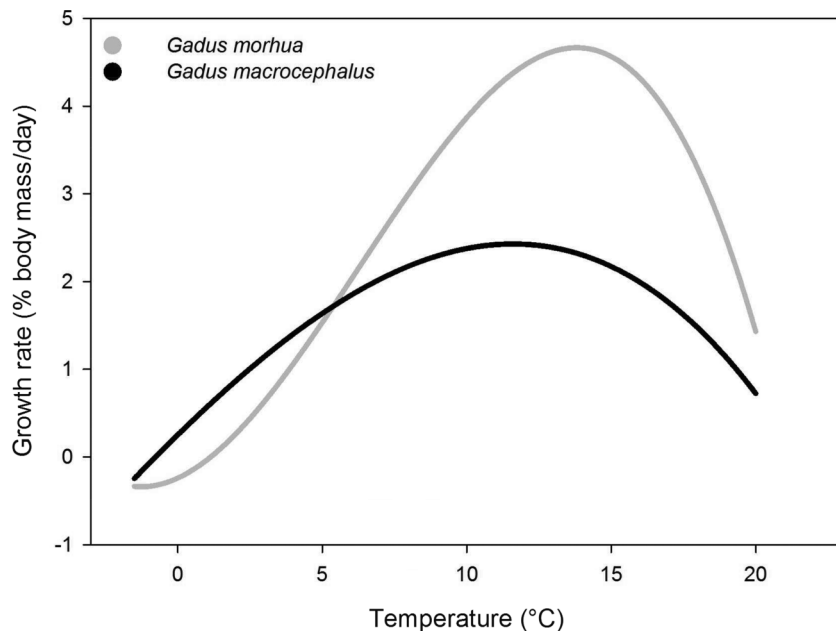

Fig. 4. Predictive strength (mean R^2 values) between time series of age-0 *Gadus morhua* and *Gadus macrocephalus* abundance measured upon arrival in nearshore areas by beach seine and abundance measured at progressively longer time spans from the initial estimate by either the beach seine (white area) or other regional assessment gear (gray area). Overall, Newfoundland age-0 gadids show relatively poor forecasting performance after 1 year relative to other areas and are notably lower than Alaskan and Norwegian forecasts. Each point represents the full time-series relationship for that region and species. Error bars (±SD) represent the variance among embayments–fjords for that region. See Table 1 for details on data.
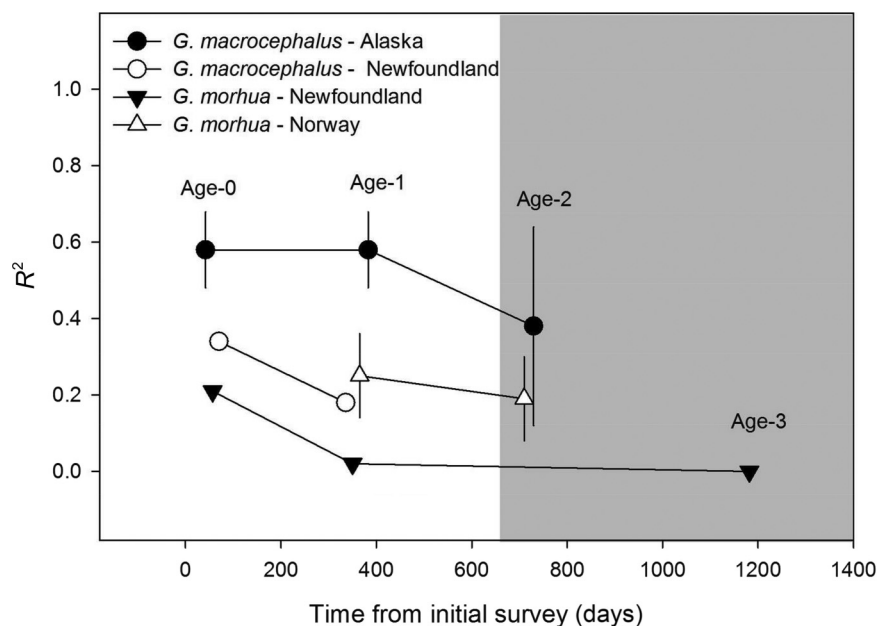
late age-0 survey indices), although these relationships varied substantially between species and regions. *Gadus macrocephalus* from Newfoundland (R^2 = 0.34) and Alaska (R^2 = 0.55) showed relatively strong relationships between early and late age-0 indices, but the predictive strength of the signal steeply declined in Newfoundland over winter (age 0 to age 1); that is, age-1 prediction (Fig. 4). For *G. morhua*, the prediction strength was weakest in Newfound-

land, being relatively low initially from early to late age-0 fish (R^2 = 0.21) and declining to <0.1 into age 1, after their first winter and subsequently into the inshore age-3 components of the 2J3KL population assessment (Fig. 4). In contrast, the predictive strength of age-0 fish to age-1 fish was relatively higher in Norway (R^2 = 0.26), as was the prediction into the North Sea assessment of age-2 fish (R^2 = 0.19; Fig. 4).

Fig. 5. Predictive strength of forecasting gadid abundance from various life stages by region. In each system, age-1 fish are a better index of recruitment than age-0 fish, although this is not as apparent in Kodiak (Alaska) where overwintering conditions are mild. Each point represents the full time-series relationship for that region and species. Note that *Gadus macrocephalus* data are not shown for Newfoundland because recruits are not assessed. Error bars (±SD) represent the variance among embayments–fjords for that region. See Table 1 for details on data.
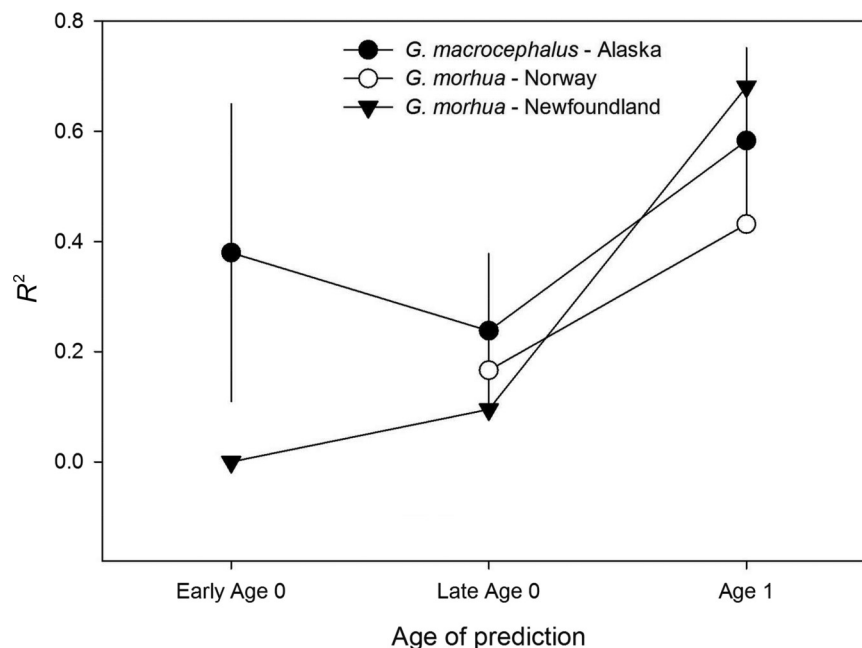
When indices of abundance of different ages of fish from coastal surveys were used to predict the future strength of year classes recruiting into the fishery, prediction strength improved for all areas when older (age-1) fish were used as the predictor (Fig. 5). Signal strength of the abundance of fish recruited into the fishery was poor when using age-0 cod indices in Newfoundland (R^2: 0–0.10), slightly improved in Norway (R^2: 0.17), and was best in Alaska (R^2: 0.23–0.38; Fig. 5). The strongest recruitment signal occurred when using indices based on age-1 abundance in Newfoundland ($R^2 = 0.68$), followed by Alaska ($R^2 = 0.49$) and Norway ($R^2 = 0.43$). The improvement in predictive strength associated with older fish was most notable for Newfoundland.

Growth potential

Growth potential varied within and among regions, with high variation among years within each region (Figs. 6 and 7). In many instances, regional growth potential was maximized (G_{max}) during the summer at ~4.5% mass·day^{-1} in *G. morhua* and ~2.5% mass·day^{-1} for *G. macrocephalus*. The statistical model indicated a significant interaction between season and region for growth potential of each species (Fig. 8; *G. morhua*, $F_{[1,49]} = 118.86$, $p < 0.001$; *G. macrocephalus*, $F_{[1,51]} = 82.96$, $p < 0.001$). The interaction was driven by the larger difference between summer and winter growth potential in Newfoundland compared with both Alaska and Norway. The low winter growth potential of Newfoundland also corresponded with the smallest size-at-age for *G. morhua* and *G. macrocephalus* among regions (Fig. 8). Evidence of upper thermal stress in the summer was also apparent in both Newfoundland and Norway but not Alaska (Figs. 6 and 7). Summer growth stress was most pronounced in Norway but appeared to be a recent phenomenon (Fig. 9); STARS analysis detected a lower significant shift in summer growth potential after 2001 ($p < 0.05$). This shift was associated with a weakening in the relationship between age-0 and age-1 abundance indices in Norway relative to the previous eight decades (Fig. 9). We detected concurrent declines in 10-year moving correlations between age-0 and age-1 abundance with average summer growth conditions beginning in the 1980s.

Discussion

High interannual variation in age-0 cod settlement was observed in each regional time series. However, our comparative analysis supported our hypothesis in that (*i*) recruitment signals improved when we used larger age-1 juveniles in each species and region, and (*ii*) variability within and among regions was strongly linked to age-0 growth potential. In Alaska, where overwintering growth potential was highest, we observed only a modest improvement in recruitment prediction using older juvenile stages. In contrast, the most pronounced improvement in recruitment signals was observed in the Newfoundland system where growth potential during the winter period was near zero. The within-region analysis of Norway also indicated that poor growth conditions in the past decade were coupled with reduced recruitment prediction. Collectively, these data indicate to us that there is high variability in the summer and winter growth potential among regions, and rapid growth between settlement and the first overwintering leads to higher survival and consequently an earlier recruitment index for coastal cod.

Growth potential and recruitment signals

Our results are consistent with a growth–survival paradigm (Anderson 1988), in that accelerated growth through early life stages reduces predation mortality and results in an increased likelihood of survival to adulthood (e.g., Houde 2008). This paradigm has been explained by both size (e.g., the "bigger-is-better" hypothesis; Miller et al. 1988) and time (the "stage-duration" hypothesis; Houde 1989; Chambers and Leggett 1992). As size and time are collectively expressed as growth rate, it follows that measurements of fish growth (either directly or indirectly) are a potential index of future survival. The growth–survival paradigm is an implicit mechanism by which temperature regulates marine fish assemblages (Attrill and Power 2002). However, temperature alone has yielded mixed results when used for recruitment prediction in gadids, with improvement in some species and systems (e.g., Bering Sea walleye pollock: Bailey et al. 2005; Mueter et al.

Fig. 6. Modeled growth potential of age-0 juvenile Atlantic cod (*Gadus morhua*) in Norway and Newfoundland based on temperature-dependent growth models (see Fig. 3) and daily regional temperature conditions from 1998 to 2012.
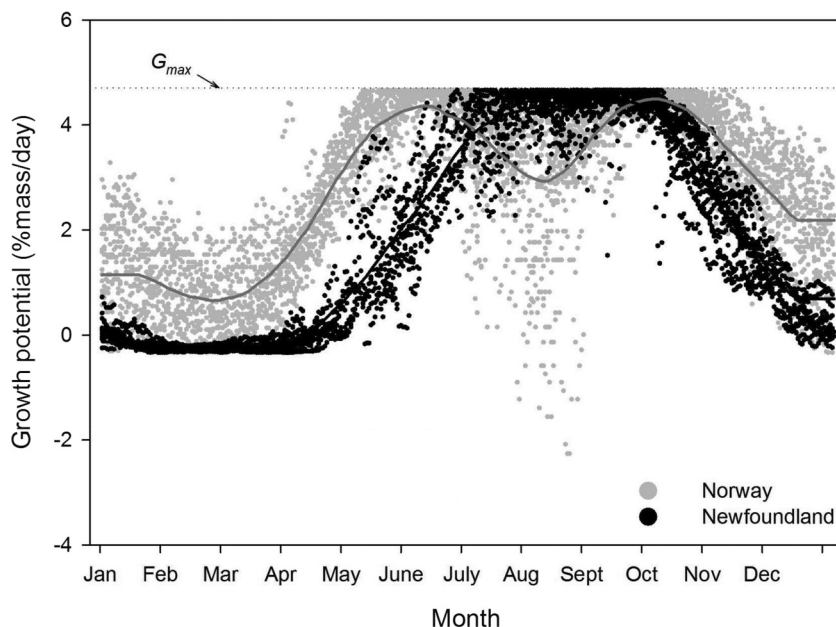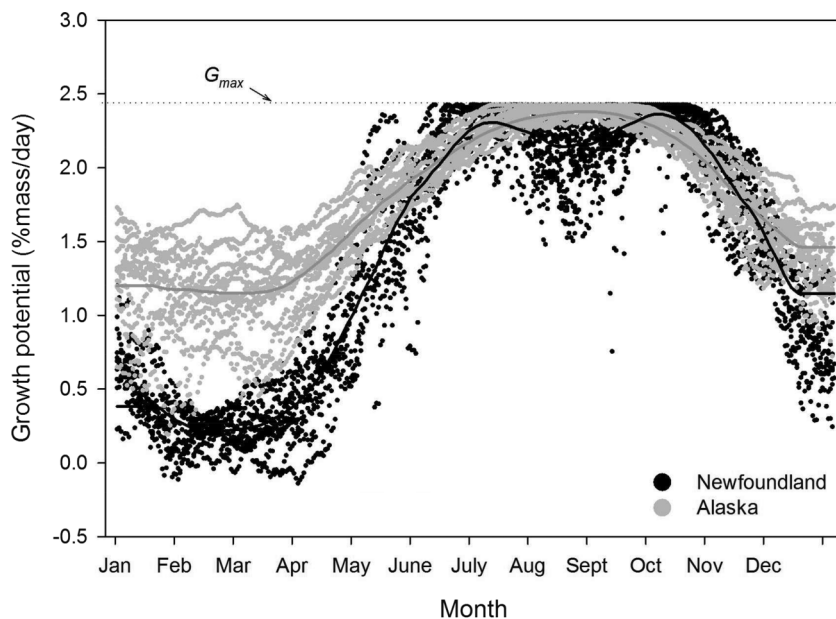

Fig. 7. Modeled growth potential of age-0 juvenile Pacific–Greenland cod (*Gadus macrocephalus*) in Newfoundland (Bonavista Bay) and Alaska (Kodiak region) based on temperature-dependent growth models (see Fig. 3) and daily regional temperature conditions from 1998 to 2012.


2006, 2011; Northeast Atlantic haddock: Stige et al. 2013) and minor to no improvement in others (e.g., Gulf of Alaska walleye pollock: Stige et al. 2013). The mixed results undoubtedly stem from a combination of measurement error and various other unmeasured environmental and biological variables. However, the results from our research suggest that temperature is a "dual-edged sword" in seasonal coastal systems, with changing growth sensitivity across regions, species, and times of year. For instance, *G. morhua* experience little summer growth variability in Newfoundland (often 95%–100% G_{max}) compared with Norway (0–100% G_{max}). Such differences are not driven by the magnitude of temperature variation within each region, but rather by the differences in summer baseline temperatures.

Mean summer temperatures in Norway are beyond the asymptotic region of the *G. morhua* growth curve, and consequently cod in Norway are more sensitive to temperature variation than cod in Newfoundland, where baseline temperatures are at or near the asymptote of the growth curve. Therefore, linear correlates of growth (e.g., temperature) may be too insensitive to capture temperature effects in coastal cod populations, which appear instead to be best defined by nonlinear growth functions. This indeed appears to be the case in Norway where temperature has a positive effect on growth in the winter–spring and a nonlinear effect on growth during the summer (Rogers et al. 2011). Species-specific physiological growth considerations (this study) not only account for such differences, but also provide a hypothesis-based approach for

Fig. 8. Mean (1 SD) growth conditions for gadids in summer and winter by region. Values represent mean summer (solid fill) and winter (hatched fill) growth potential of juvenile gadids by region from 1998 to 2012. Summer values are based on 8 weeks of temperature-dependent growth following settlement. Winter values are based on 16 weeks of mean annual growth between 1 January and 1 May in each system. Mean size at age 1 (circles) is indicated for each region (1 SD).
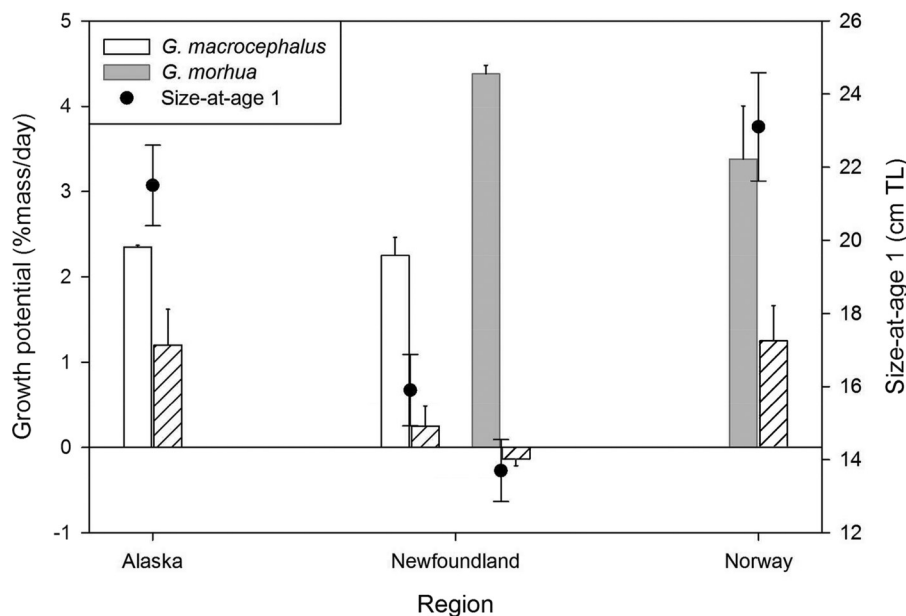
examining seasonal temperature effects within and across regions. Further refinement of these approaches should also consider population-specific growth, as genetic analysis of age-0 cod collected in the Skaggerak seine survey indicates the presence of two distinct groups: (*i*) a population of North Sea origin that tends to be larger and more common in outside fjords and (*ii*) a local population that tends to be smaller and more common in the interior fjords (H. Knutsen, Institute of Marine Research, unpublished data). The mechanisms driving these patterns are not fully understood (e.g., growth differences or settlement timing), but the observation raises important questions as to how the genetically determined growth response might impact recruitment signals and population structure as thermal habitat changes within a region.

We used the models of growth potential to characterize and compare each ecosystem rather than attempting to improve within-region recruitment prediction. In Newfoundland and Alaska, preliminary analyses of the residuals of the annual recruitment index with summer and winter growth conditions did not reveal significant trends worth further exploration (not shown here). We suspect that temperature-dependent growth potential sets the scope for year-to-year growth in these regions, but "realized growth" by individuals is dependent on annual changes in food availability and energetic intake (Jobling 1988), possibly further modified by density in juvenile cod (Rogers et al. 2011; Laurel et al. 2016). However, despite this obvious concern, long time-series analysis of coastal cod in Norway indicated that temperature-dependent growth potential can impact within-region recruitment dynamics. In Norway, age-0 and age-1 abundance indices have historically been tightly linked (Tveite 1992). However, this relationship has weakened as summer growth conditions have deteriorated in the last decade. Summer nearshore water temperatures have often exceeded 20 °C and corresponded with observations of reduced growth in age-0 cod during this period (Rogers et al. 2011). However, the mechanism by which temperature-dependent growth potential impacted recruitment signals in Norwegian coastal waters remains uncertain. Studies on offshore North Sea cod suggest that there is a direct temperature effect on recruitment, but also a stronger indirect effect caused by temperature-induced shifts in

the plankton community and hence food availability for cod larvae (Beaugrand et al. 2003; Olsen et al. 2011). Beach seines are also prone to measurement error, as they are spatially limited to relatively shallow water where the temperatures are highest. While age-0 fish are generally constrained in their habitat use, older (age-1+) fish may seek thermal refugia in deeper water and thus be less vulnerable to shore-based sampling gear in warm years (Freitas et al. 2015). Regardless of the mechanism, these results suggest that climate-induced changes in growth conditions may strengthen or reduce recruitment signals contained in juvenile surveys.

The settlement dynamics of *G. morhua* in Newfoundland may partially explain why recruitment forecasting from early age-0 indices in this population is relatively poor. Rather than a single settlement event, age-0 Atlantic cod arrive at the Newfoundland coast in a series of two or more "recruitment pulses" that span across the entire summer and fall period of the beach seine survey (Gregory et al. 2006; Ings et al. 2008). This may explain our observations suggesting early age-0 estimates did a relatively poor job of predicting late age-0 estimates for *G. morhua* compared with *G. macrocephalus*, which settle as a single recruitment pulse (Ings et al. 2008). Secondly, the continued arrival of newly settling age-0 *G. morhua* juveniles results in high size variation of juvenile cod entering their first overwintering period; for example, 35–120 mm SL (Gregory et al. 2006). Based on laboratory results, mortality rates in the smaller overwintering cod (i.e., 50–60 mm, late recruitment pulse) are three to four times higher than those for larger cod (80–90 mm) (Gotceitas et al. 1999). Despite the potential for selective mortality on small age-0 individuals, age-1 cod sizes in Newfoundland were still found to be 30%–40% smaller than age-1 cod in Norway and Alaska. Therefore, future scenarios in which settlement dynamics change or winter growth conditions improve will likely be a key component of higher first year survival in Atlantic cod, leading to improved forecasting of year-class strength from age-0 coastal cod collected from nearshore coastal waters.

In conclusion, nearshore surveys offer a logistically effective means of sampling juvenile cod, but their ability to forecast future recruits to harvestable populations is highly variable among regions. In Norway and the Gulf of Alaska, recruitment signals were

Fig. 9. Changes in age-0 growth potential and correlations between age-0 and age-1 abundance of Atlantic cod (*Gadus morhua*) from an 88-year time series along the Skagerrak coast of Norway. Top panel indicates annual values of summer growth potential, and bottom panel indicates recruitment correlation along with summer growth potential (10-year moving average each). The gray area indicates a significant negative shift in summer growth potential as detected by sequential *t* test analysis of regime shifts (STARS). Correlations between age-0 and age-1 abundance indices before and after the shift are shown. The bottom panel shows 10-year moving correlations in recruitment along with the 10-year moving average summer growth potential.
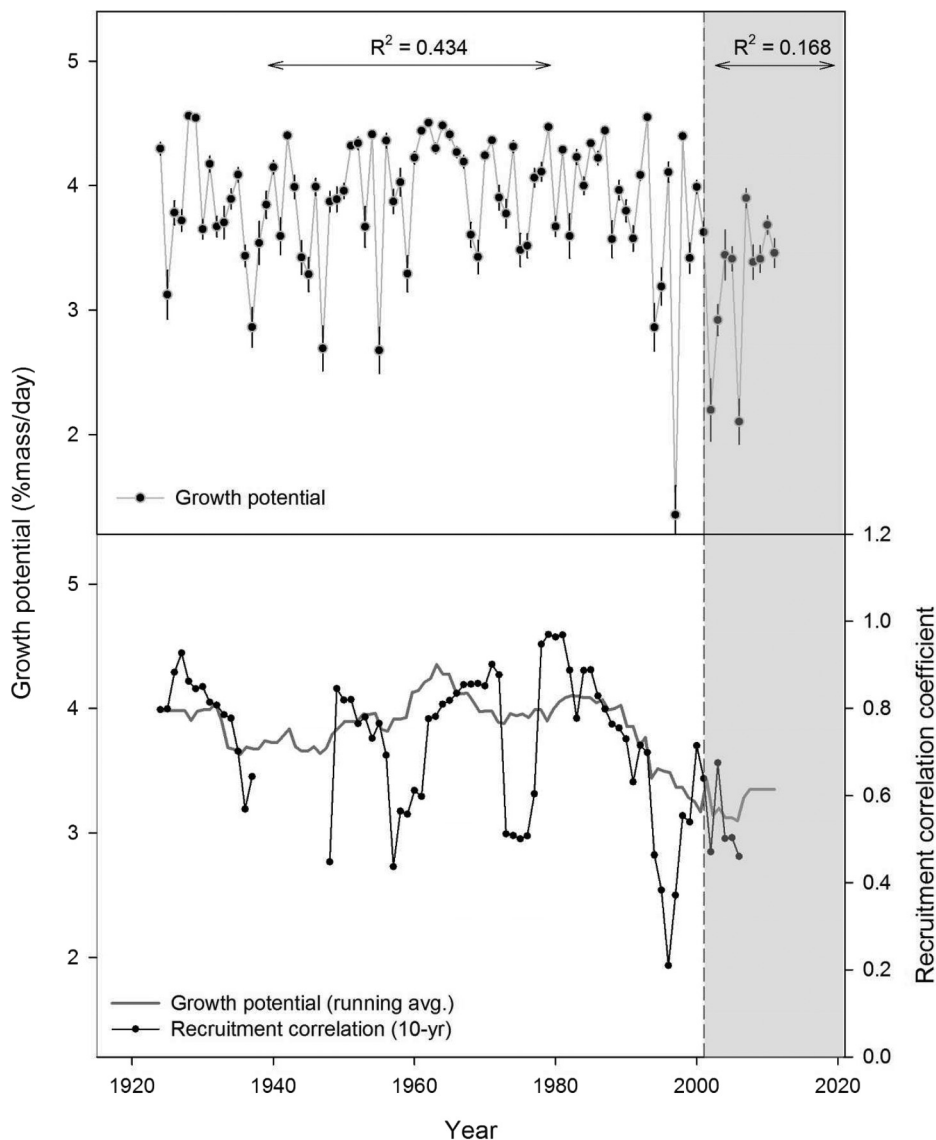
more apparent in the age-0 stage compared with Newfoundland, a more subarctic ecosystem, where these signals were comparatively weak; Newfoundland recruitment signals markedly improved only after the first overwintering period as age-1 fish. The variable predictive strength of age-0 assessments should not dissuade continued monitoring or attempts to incorporate such surveys into stock assessment and recruitment forecasting, particularly since the same surveys also provide indices of age-1 abundance. Coastal time series contain some of the only direct information on age-0 stages of cod species, critical towards capturing and understanding climate related changes in regional population dynamics. Coastal ecosystems are particularly vulnerable to changing physical environments as the result of climate change because of their complex trophic dynamics and potential for wide temperature fluctuations ([Harley et al. 2006](#)); growth habitats for fish with shallow-water dependence will undoubtedly change with increased mean water temperatures. The impact on economically and eco-

logically important species like Atlantic and Pacific cod will likely be region-specific, but will only be measured and understood by using regionally relevant time series spanning the period these environmental changes are manifested.

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sity of Newfoundland. In Alaska, data collection was supported by the Habitat and Ecological Processes Research (HEPR) Program, Alaska Fisheries Science Center. This study is NPRB contribution No. 596. The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA.

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