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## Spawning phenology and geography of Aleutian Islands and eastern Bering Sea Pacific cod (*Gadus macrocephalus*)



Sandra K. Neidetcher<sup>a,\*</sup>, Thomas P. Hurst<sup>b</sup>, Lorenzo Ciannelli<sup>c</sup>, Elizabeth A. Logerwell<sup>a</sup>

<sup>a</sup> Fishery Interaction Team, Resource Ecology and Fisheries Management Division, Alaska Fisheries Science Center, National Marine Fishery Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115, USA

<sup>b</sup> Fisheries Behavioral Ecology Program, Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center,

National Marine Fishery Service, National Oceanic and Atmospheric Administration, Hatfield Marine Science Center, Newport, OR 97365, USA

<sup>c</sup> College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA

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### ABSTRACT

Pacific cod (*Gadus macrocephalus*) is an economically and ecologically important species in the south-eastern Bering Sea and Aleutian Islands, yet little is known about the spawning dynamics of Pacific cod in these regions. To address this knowledge gap, we applied a gross anatomical maturity key for Pacific cod to describe temporal and spatial patterns of reproductive status over three winter spawning seasons: 2005, 2006, and 2007. Maturity status of female Pacific cod was assessed by fishery observers during sampling of commercial catches and used to construct maps showing spawning activity in the Bering Sea and Aleutian Islands. Most spawning activity was observed on the Bering Sea shelf and Aleutian Island plateaus between 100 and 200 m depth. Data for those days when a high percentage of spawning stage fish were observed were used to identify areas with concentrations of spawning fish. Spawning concentrations were identified north of Unimak Island, in the vicinity of the Pribilof Islands, at the shelf break near Zhemchug Canyon, and adjacent to islands in the central and western Aleutian Islands along the continental shelf. The spawning season was found to begin in the last days of February or early March and extend through early to mid-April. Variation in spawning time (averaging ~10 days between years) may have been associated with a change from warm (2005) to cold (2007) climate conditions during the study period. Our information on Pacific cod spawning patterns will help inform fishery management decisions, models of spawning and larval dispersal and the spatial structure of the stock.

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### 1. Introduction

The timing and location of spawning are central components that define a species' reproductive strategy (Petitgas et al., 2010). The spawning site provides the initial conditions for development of early life stages. Spawning site features such as topography and bathymetry set the landscape in which recruitment processes unfold (Ciannelli et al., 2007), while meteorological and oceanographic cycles interacting with site features determine the physical conditions present during this critical period. The location and timing of spawning is assumed to be coupled, through natural selection, to ecological conditions beneficial for early life survival (Leggett, 1985) such as high concentration of prey and the dispersal potential of eggs or larvae (Cushing, 1969). Though the specific mechanisms determining the timing and location of marine fish spawning are poorly understood (Cury, 1994), recent experiments assessing interactions

between environmental conditions and spawning found initial oocyte development aligned with the timing of earth's equinox and the progression of oocyte development related to ambient temperatures (Kjesbu et al., 2010; Olive et al., 1998). Knowledge of spawning patterns is also important for assessment of spawning migrations, identification of early life stage distribution and patterns of dispersal to juvenile nurseries, and understanding of population structure (Hjort, 1926; Sinclair and Iles, 1988).

Pacific cod, *Gadus macrocephalus* range from the Sea of Japan across the North Pacific Rim to the California coast (Hart, 1973) and is an important groundfish species in Alaska. Pacific cod are predators of other demersal fishes (primarily walleye pollock, *Gadus chalcogrammus*) and crustaceans such as crab (Livingston and deReynier, 1996) and are prey for top predators, including endangered Steller sea lions (*Eumetopias jubatus*) (Sinclair and Zeppelin, 2002). Commercial Pacific cod catches from the Bering Sea and Aleutian Islands averaged 200,000 metric tons from 2001 to 2009 with an average annual value of US\$120 million. Pacific cod catches in the Bering Sea and Aleutian Islands are second only to that of walleye pollock (Hiatt et al., 2011).

\* Corresponding author. Tel.: +1 206 526 4521; fax: +1 206 526 6723.  
E-mail address: [Sandi.Neidetcher@noaa.gov](mailto:Sandi.Neidetcher@noaa.gov) (S.K. Neidetcher).

**Table 1**

Visual maturity stage descriptions for female Pacific cod.

Anatomical stage	Anatomical stage description
Immature	Small, pink or transparent, no oocytes visible to eye.
Developing	Small to $\frac{1}{2}$ the length of the abdominal cavity, well-developed blood vessels, oocytes distinct and visible through ovary wall, coloration yellow to bright orange. Oocytes difficult to separate.
Prespawning	Ovaries are greater than $\frac{1}{2}$ the abdominal cavity. The ovary surface is translucent and mottled grayish. Oocytes are opaque and less adhesive.
Spawning	Ova run under light pressure to the abdomen.
Spent	Gonads appear flaccid and watery. Ovaries may contain remnants of disintegrating ova and blood.
Resting	Ovaries are small and firm, may have black or silver coloration on surface. No oocytes are visible to eye.

In the Bering Sea and Aleutian Islands, Pacific cod inhabit the continental slopes and shelf, most often at depths to 300 m (Bakkala, 1984). Conventional mark and recapture efforts have demonstrated that adult Pacific cod are distributed across the continental shelf during summer and are found in dense spawning aggregations along the continental slope and shelf near Unimak Island and the Pribilof Islands during late winter (Shimada and Kimura, 1994). While several areas with large spawning aggregations have been identified, broad-scale surveys of spawning distribution have not been conducted in Alaskan waters, thus comprehensive information on the timing, locations, and depth of spawning are not well-described in the Bering Sea and Aleutian Islands regions. In Washington's Puget Sound, spawning was found to occur at depths of 40 to 265 m (Palsson, 1990), confirming earlier reports of spawning in shallow coastal areas (Karp, 1982). In British Columbia, Pacific cod have a short spawning season which occurs in the late winter and early spring (Foucher and Westrheim, 1990). Studies have suggested that spawning occurs slightly later at higher latitudes (Westrheim, 1996). Pacific cod stocks along the Asian coast also show variable spawning patterns related to latitude with migration patterns of northern stocks linked to local currents and temperature patterns (Savin, 2008). Northern stocks off the Russian coast move off-shore to spawn in warmer water at deeper depths in the late winter while the southern stocks off the Korean coast spawn in the seasonally warmer near-shore waters (Moiseev, 1960).

Pacific cod is a broadcast spawning species that releases approximately 1,000,000–1 mm diameter eggs per individual annually (Westrheim, 1996). Ovarian development is synchronous and eggs are released in a single batch (Stark, 2007; Sakurai and Hattori, 1996; Bowden et al., 1990). Because Pacific cod eggs are demersal (Thompson, 1963), they are rarely captured during ichthyoplankton surveys. Therefore, data from extensive annual ichthyoplankton surveys in the southeastern Bering Sea have not been used to infer spawning patterns in this species (Matarese et al., 2003; Smart et al., 2012). With these sampling limitations and a general lack of life history research effort focused on this species, little is known about the spawning patterns of adults or the distribution and movement patterns of early life stages (but see Hurst et al., 2012; Parker-Stetter et al., 2013).

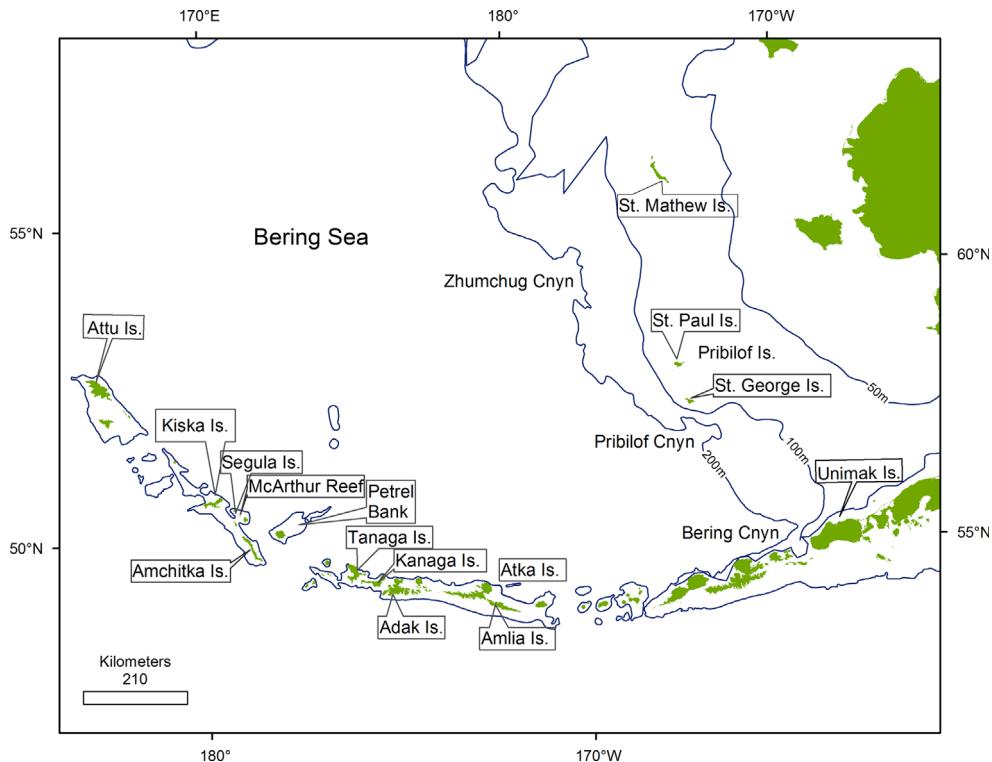
Anatomical maturity keys characterize gross morphological changes of the ovaries to estimate reproductive maturity. Maturity keys are commonly used to study the onset and duration of the spawning season by determining the reproductive condition of adult fishes (Parenti and Grier, 2004; Hunter and Macewicz, 2003; West, 1990). However, maturity keys have been criticized for their subjectivity with key descriptions based on ovary characteristics such as color and relative size which may be interpreted differently among users. Additionally, because ovaries mature gradually, users often have difficulty in accurately identifying ovaries in transitional stages of development (West, 1990). Stark (2007) was critical of macroscopic maturity keys for Pacific cod because

ovaries showing very early development can be classified as immature when examined visually. However, when validated against maturity stages based on histological examination of individual oocytes, maturity keys can provide a robust description of maturity states, and are especially useful in identifying later stages of maturity for single-batch spawning fishes. Further, through the application of an anatomical maturity key, researchers are able to assess significantly larger numbers of fish than would be practicable based on traditional histological analyses. Recent advances in applying shape analysis software to measure oocyte size show promising research in oocyte development (Thorsen and Kjesbu, 2001). However, these methods still require chemical fixation and laboratory processing, which makes them less practicable in some fishery-dependent sampling programs.

For this study we applied a maturity key developed specifically for Pacific cod. A complete description of the ovary characteristics and key development and validation are described in Neidetcher (2012). The key identifies changes in the gross appearances of ovaries (size, color, adhesion of oocytes in the ovary) that characterize changes that occur with the progression of the spawning season. The resulting gross anatomical maturity key for female Pacific cod includes the following stages: (1) Immature, (2) Developing, (3) Prespawning, (4) Spawning, (5) Spent and (6) Resting (Table 1).

The accuracy of the visual maturity key was evaluated against the staging of individual oocytes based on histological processing and microscopic examination. The comparison of observer-assigned maturity stages to histologically examined oocytes from within the same fish resulted in an overall misclassification rate of 43%. However, the mismatch is narrow with most misclassifications (95%) assigned to an adjacent stage. Further, most (59%) misclassifications occurred in the early stages of egg development (between the developing and prespawning stages). Only 10% of the fish histologically-determined to be in the developing or prespawning stages were misclassified as spawning or spent (Neidetcher, 2012). Therefore, we determined that the use of the maturity key was sufficiently robust to identify broad-scale temporal and spatial patterns in spawning of Pacific cod in the Bering Sea and Aleutian Islands. Various stages and stage combinations are used for mapping spawning locations and for determining spawning phenology. Misclassification rates associated with these stages are provided with each analysis.

The objectives of this research are to describe spatial and temporal spawning patterns of Pacific cod in the Bering Sea and Aleutian Islands. Gross anatomical maturity of female Pacific cod was assessed by fishery observers monitoring catch aboard commercial fishing vessels in the eastern Bering Sea and Aleutian Islands during three winter spawning seasons (2005–2007). Observers applied a visual maturity key developed for Pacific cod and validated against histological samples (Neidetcher, 2012). The broad spatial and temporal scale of sampling allowed for a comparison of spawning patterns from fished locations across



**Fig. 1.** Sampling locations in the eastern Bering Sea and Aleutian Islands where commercial fishery observers collected maturity information about Pacific cod.

the eastern Bering Sea and Aleutian Islands and over years with varying climate conditions.

## 2. Methods

### 2.1. Study area

The eastern Bering Sea slope separates the eastern Bering Sea diagonally from the southeast to the northwest into a shallow shelf and a deep-water basin (Fig. 1). The Aleutian Islands Archipelago is a string of volcanic islands separated by deep-water passes, marking the southern border of the Bering Sea. The island ridge, which intersects the slope at Unimak Island, is mostly comprised of a narrow continental shelf and steep slope. Conversely, the Bering Sea is dominated by a broad, flat continental shelf intersected by submarine canyons along the shelf break. The southernmost canyon, the Bering Canyon, breaches the slope at the intersection of the shelf and the Aleutian Island arc and Unimak Pass. The Pribilof Canyon cuts into the slope just south of the Pribilof Islands, while the Zhemchug Canyon is situated over 200 km to the northwest.

### 2.2. Data collection

Pacific cod maturity data were collected by fishery observers trained by the Alaska Fisheries Science Center's (AFSC) Fisheries Monitoring and Analysis Division (FMA). Observers used the maturity key to assess the maturity status of fish captured in fisheries specifically targeting Pacific cod and in fisheries that caught cod as incidental catch during operations directed to other species. The capture gear in the sampled fisheries included mid-water and bottom trawls, longlines, and pots. Prior to the at-sea operations, observers were trained in the use of the maturity key.

A random sampling protocol was used to select a subset of commercial catches (hauls) from which fish were selected for

gender identification and measured for length. Most observers assessed the maturity of all fish specimens used for these gender and length collections. Additionally, some observers opportunistically sampled fish from hauls that were not assessed for biological characteristics when Pacific cod were available in those hauls. Random selection techniques were maintained in choosing individual fish for analysis from these additional hauls. Details concerning observer sampling protocols are available in the AFSC's North Pacific Groundfish Observer Manual (AFSC 2005–2007). To assess gonad maturity, the abdominal cavity was opened and characteristics of the surface of the ovaries and condition of individual oocytes were compared to descriptions and digital photographs provided in the maturity key. In addition to biological characteristics, observers recorded the date and location (latitude and longitude measured to degrees and minutes) of the fishing event. On vessels using trawl gear, capture locations recorded the point at which the gear is retrieved from fishing depth. For fixed-gears, the recovery location was typically the end of the gear string. Strings of pots and longlines of individual fishing hooks were often several kilometers in length.

Pacific cod maturity status was evaluated by fisheries observers through three winter spawning seasons: 2005, 2006, and 2007. In each spawning season, sampling began in early January and continued through April. Regional climate conditions varied markedly across the three sampling years: water temperatures were anomalously high in 2005, while 2006 was a year of transition to a colder regime (Rodionov et al., 2007). The sea ice extent for 2007 was one of the greatest on record reaching the outer Bering Sea shelf, the Pribilof Islands, and the Alaska Peninsula east of Unimak Island.

### 2.3. Data analysis

Using Geographic Information System (GIS) software, the catch locations for observer-assessed prespawning and spawning stage fish were plotted to display the locations of spawning Pacific cod

captured by the fishery. The prespawning stage occurs for a short period of time prior to egg hydration and spawning, therefore the location of fish at this stage is assumed to be in the vicinity of the spawning grounds. Pooling prespawning and spawning stages for this analysis reduced misclassification rates between histological analysis and visual assessment to 18%. Because rules of confidentiality apply to protect commercial fishing information, haul locations were binned according to a 20 × 20-km grid system. To avoid revealing catch locations for any given fishing vessel, data in grid cells with fewer than three vessels were excluded.

We identified concentrated spawning activity by: (1) identifying days when > 15% of fish sampled were classified as spawning; and (2) identifying locations where spawning fish were caught on those days. A daily percent spawning was calculated by dividing the number of spawning stage fish identified by observers by the number of fish examined each day over all geographical areas sampled that day. Days with 15% or greater spawning fish were identified as high spawning activity days. The maps show the capture locations during days when observers identified concentrated spawning. Because locations of concentrated spawning occurred in areas with high levels of sampling effort, rules of confidentiality did not prevent the public identification of these locations.

Temporal patterns in spawning were examined by grouping maturity stages to determine when oocyte maturation transitioned into, and past, the spawning stage. The fraction of fish determined to be in developing and prespawning stages were combined and plotted against the combined fraction of fish in the spawning and spent stages. The misclassification rate between these combined stages was only 3% (Neidetcher, 2012). Fish classified as immature or resting were omitted from this analysis. Collections from January 1 to April 30 were pooled into 5 day intervals to illustrate the general pattern over the spawning season. The beginning of the spawning season was defined as the time when the percent of spawning+spent stage fish reached 20% of sampled individuals; the end of the spawning season was defined as the time when this percentage reached 80%. Values between 40 and 60% defined the mid-spawning period.

### 3. Results

#### 3.1. Observer-assessed maturity collections

Between 2005 and 2007, fishery observers determined the maturity status of 37,268 female Pacific cod (Table 2). This was accomplished through the use of an anatomical maturity key, applied by approximately 300 fishery observers aboard 152 commercial fishing vessels operating in the Bering Sea and Aleutian Islands over three years. Sampling levels were highest during 2005, remained high in 2006, and declined in 2007 because fewer observers participated in the project. In general, the proportion of fish assigned to each maturity stage was similar for the three study years, suggesting that there were no systematic differences in the interpretation of the maturity key by observers among years.

**Table 2**

Gross anatomical maturity stages for female Pacific cod assessed by observers from January 1–April 30 aboard commercial fishing vessels in the Bering Sea and Aleutian Islands.

Year	No. Obs.	Immature	Developing	Prespawn	Spawning	Spent	Resting	Total
2005	76	3352(23)	2947(20)	4875(33)	857(6)	1285(9)	1385(9)	14,703
2006	81	3505(26)	3080(23)	4927(37)	838(6)	408(3)	655(5)	13,413
2007	58	2005(22)	2104(23)	3034(33)	470(5)	894(10)	645(7)	9152

(Parentheses show the percent of fish assigned to each maturity stage. No. Obs.=number of observers participating in the project.)

#### 3.2. Spawning locations

Annual maps of the capture locations of prespawning and spawning stage Pacific cod indicated that spawning activity was widespread, occurring predominantly on the outer shelf of the eastern Bering Sea (outer shelf domain) most often between 100 and 200 m depth. Observer sampling effort in 2005 and 2006 identified widespread spawning along the northern outer shelf from southeast of the Pribilof Islands to west of St. Matthew Island. Despite minor differences in the spatial and temporal distribution of sampling in 2007, observers identified spawning activity in similar locations along the northern outer shelf. In all three years, additional spawning areas were identified in the southern Bering Sea from Unimak Pass to Amak Island, the central Aleutian Islands from Amlia Island to Tanaga Island, and the western Aleutian Islands from Petrel Bank to Attu Island (Fig. 2: see Fig. 1 for place names).

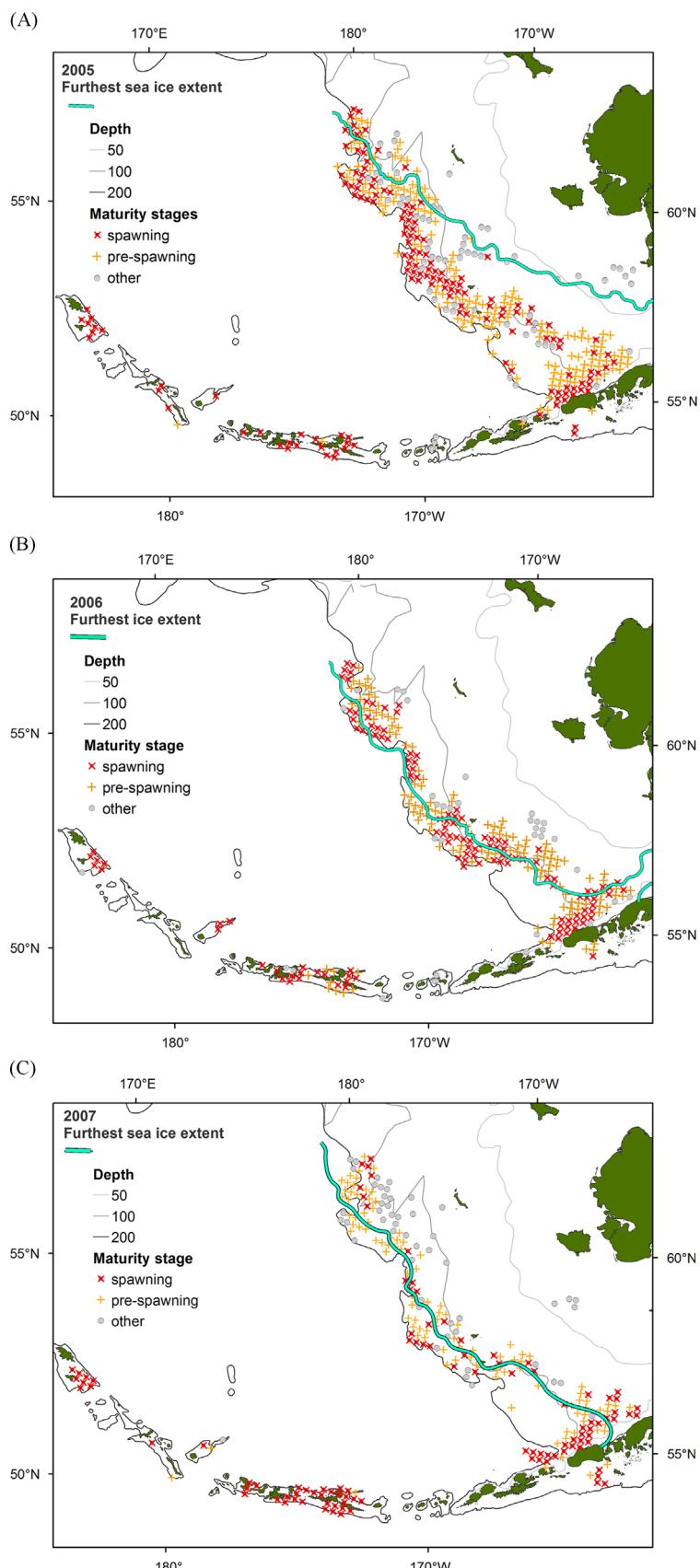
An examination of maturity stage assignments by fishing gear type from the same geographic region and time period shows reduced level of spawning stage assignments for longline gear. For example, comparison of maturity assignments from the Unimak area during peak spawning when all four gear types are deployed in this area shows 19% assignment to spawning stage by observers onboard bottom trawl vessels, but only 5% assignment to spawning stage onboard longline vessels (Fig. 3). Because longline is the primary gear type used along the northern outer shelf (Fig. 4), spawning locations in this area may be underrepresented by observer maturity assessments.

During the course of the study, spawning concentrations were identified along the Aleutian Islands, north of Unimak Island, near the Pribilof Islands, and the Bering Sea shelf edge along the 200 m isobaths (Fig. 5). Observers identified the highest percent spawning (> 35%) in 2005 in the western Aleutians at Attu Island, in the central Aleutians at Atka Island, and along the Bering Sea shelf north of Unimak Island, seaward of the Pribilof Islands and along the northern outer shelf. The percent of spawning stage fish sampled remained high at Atka and Unimak Island in 2006 (> 30%) (Fig. 5). Though observations of spawning stage fish in 2007 were low in many areas along the Bering Sea shelf break, concentrations of spawning stage fish were observed in these areas.

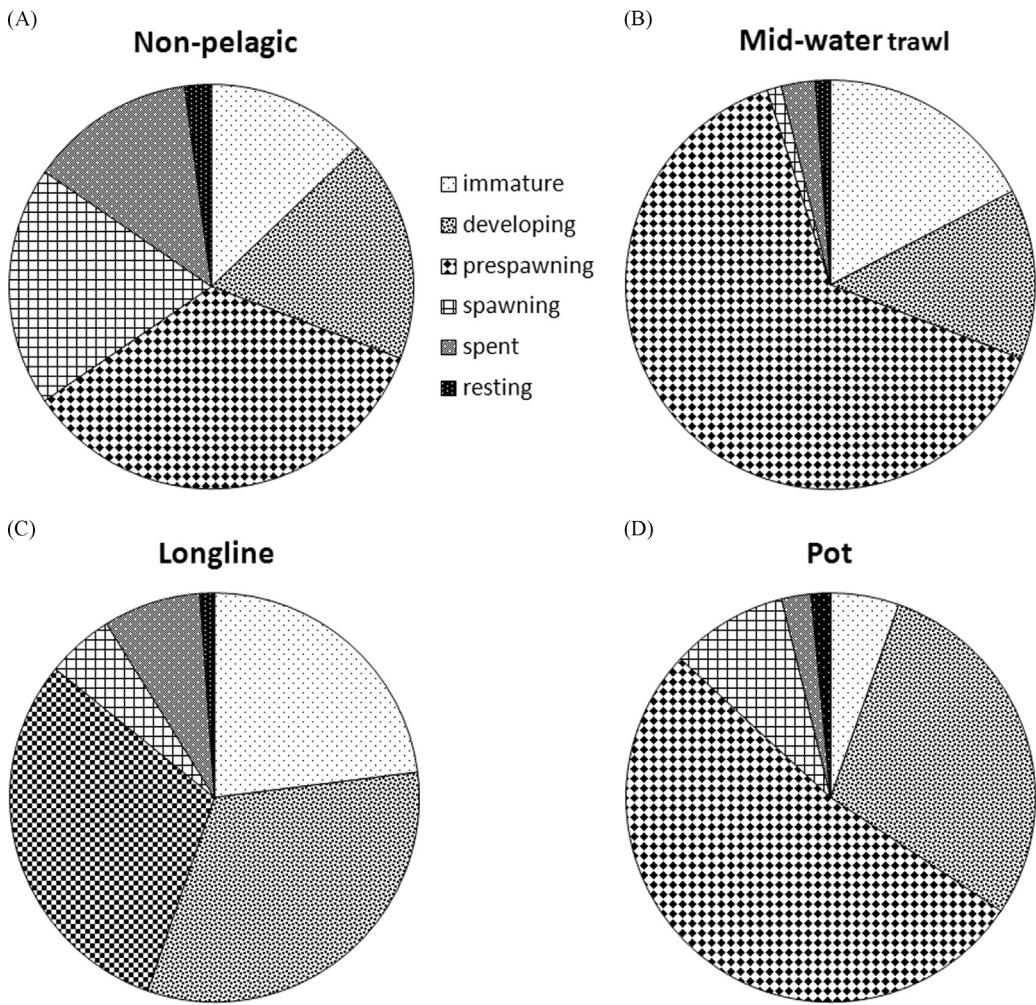
While spawning concentrations reoccur in the same general locations in the central and western Aleutian Islands and north of Unimak, their location around the Pribilof Island and along the outer shelf appeared to shift among years. Areas of concentrated spawning during 2005 occurred between the 100 and 200 isobaths seaward of the Pribilof Islands to the northern base of the Zhemchug Canyon, while these concentrations in 2006 occurred primarily east of St. George Island (southern Pribilof Island) and farther north along the shelf edge. Few spawning concentrations were detected either south or west of the Pribilof Islands in 2007, and only one area in the northern outer shelf was observed in the same year.

#### 3.3. Spawning phenology

The timing of the spawning season for Pacific cod varied slightly over the three-year sampling period. Spawning typically



**Fig. 2.** Distribution of prespawning and spawning stages of female Pacific cod from maturity data in 2005–2007 (A–C) from January–April. To avoid revealing catch locations for any given fishing vessel, multiple vessel locations were merged into  $20 \times 20 \text{ km}^2$  grid cells. The symbol x is used to indicate locations where observers identified spawning stage fish. The symbol + indicates locations where prespawning stage fish were observed in the absence of spawning stage fish. The locations of observed stages other than spawning and prespawning are indicated with circles.



**Fig. 3.** Proportion of fish at each maturity stage from the Unimak Pass area by gear type.

began in early March and persisted through early April. In 2005, the fraction of spawning+spent stage fish increased to 20% by March 1. These numbers fell between 40 and 60%, for a short period during the last week of March, and reached 80% by April 1 (Table 3). Spawning+spent stage fish reached 20% a few days earlier in 2006 than 2005. Spawning+spent stages for 2006 reached 80% by the first week of April. In 2007, spawning+spent stages did not reach 20% until the second week in March but reached 40–60% for a short period early in the third week of March, then reached 80% by the end of the first week in April. The later date at which spawning+spent stage percentages reached 20% suggested a delayed initiation of spawning in 2007 (Fig. 6). During the third week of April in 2005, observers identified a significant number of fish that had not yet spawned. These results suggest the presence of a group of late-spawning fish, though sample sizes at this time were very low. Of interest is also the fluctuating pattern of 2006, which may indicate timing differences among spawning groups (Fig. 6).

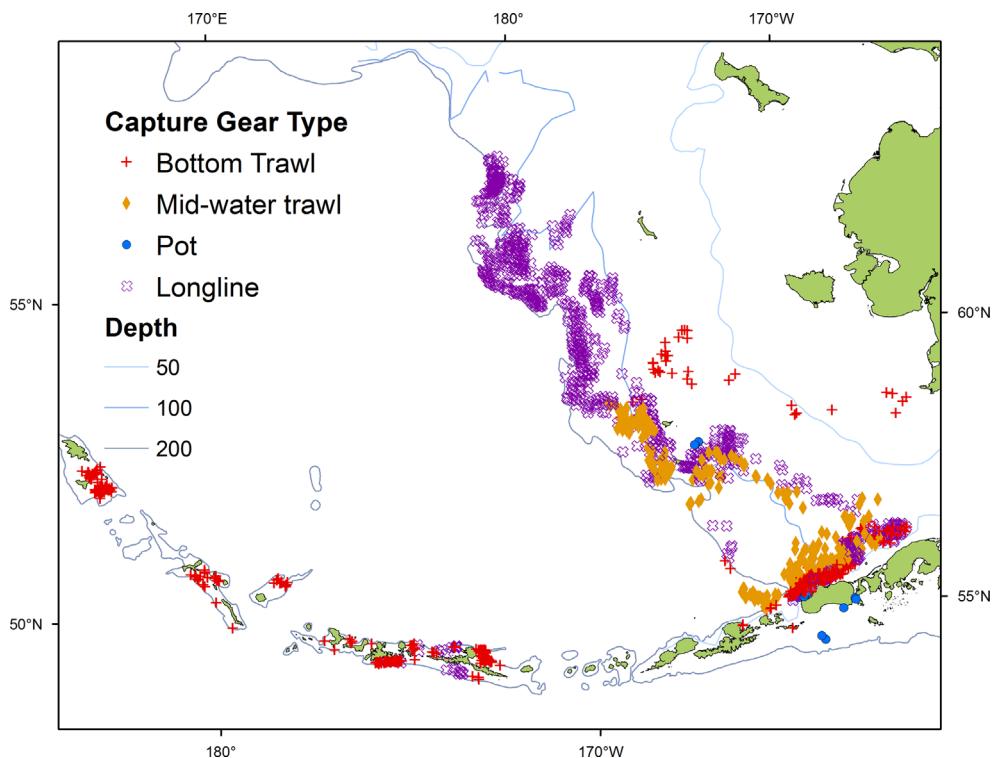
#### 4. Discussion

##### 4.1. Using observer-assessed visual maturity keys to identify spawning patterns

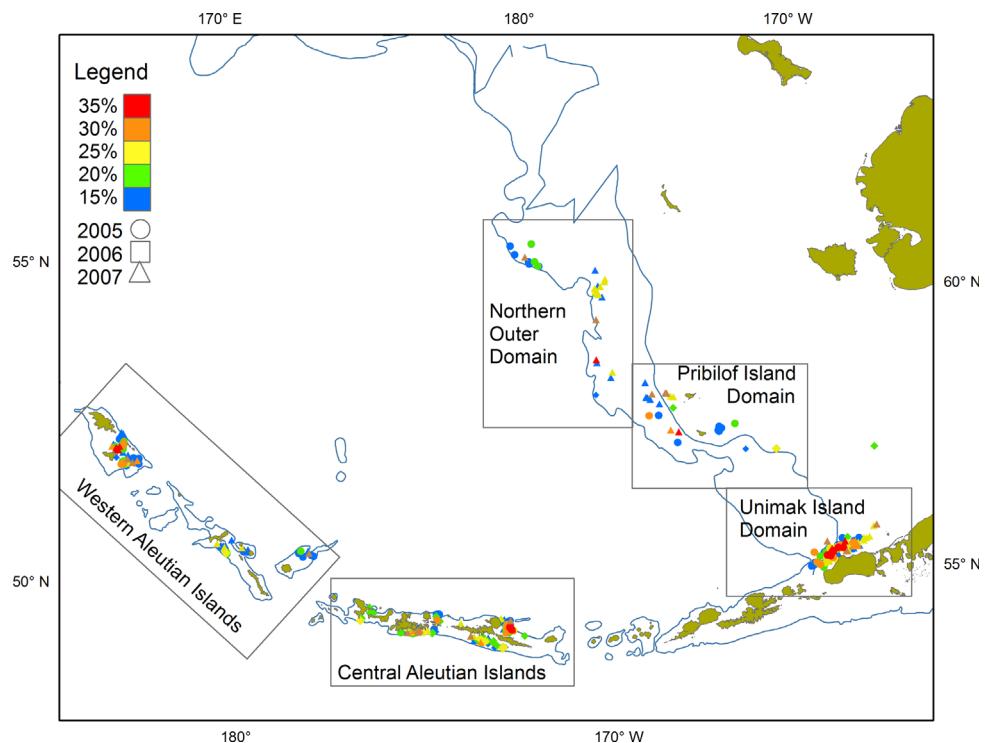
Spawning activity in this species was found to be much more widely distributed than has generally been recognized. In addition

to previously recognized spawning locations in the vicinity of Unimak Island and the Pribilof Islands, additional spawning concentrations were identified along the northern outer shelf and at sites along the Aleutian Islands. While our samples were limited to regions targeted by commercial fishing operations, it seems reasonable to assume that fishers are adept at locating harvestable fish aggregations because they are aided by advanced technologies and extensive knowledge of fish distributions. Thus our identified spawning areas likely represent broad patterns in spawning activity of Bering Sea and Aleutian Island Pacific cod. Pacific cod are most abundant on the shelf and are only rarely captured off the shelf at depths below 300 m (Bakkala, 1984). With the exception of the Bering Canyon, there was little fishing effort (and hence little sample coverage) off the slope at depths greater than 200 m, so it is unclear if Pacific cod are also spawning in the deepest parts of their range such as the outer canyons off the northern slope.

In addition, access to fishing areas on the middle shelf appears limited by sea ice cover during the winter spawning season in all but very low sea ice years. As a result, there were also few samples from shallow shelf areas of the Bering Sea in 2006 and 2007. During years with average sea ice coverage, access may be limited along the northern outer shelf, and during years with extensive sea ice coverage, sampling around the Pribilof Islands may be impacted. Sea ice coverage rarely reaches as far southeast as the Alaska Peninsula northeast of Unimak Pass (Stabeno et al., 2001). Although sampling did occur in the vicinity of the Pribilof Islands and along the shelf edge to the northwest in all three years, effort



**Fig. 4.** Catch locations by gear type for maturity data assessed by observers aboard commercial vessels in the Bering Sea and Aleutian Islands.



**Fig. 5.** Locations of concentrated spawning in the Bering Sea and Aleutian Islands for 2005–2007. Spawning concentrations locations are coded by color for daily percent spawning and by shape for sample year. Spawning stage data were plotted using unique colors for the different levels of percent spawning stage sampled, while unique shapes were used to represent sample year. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

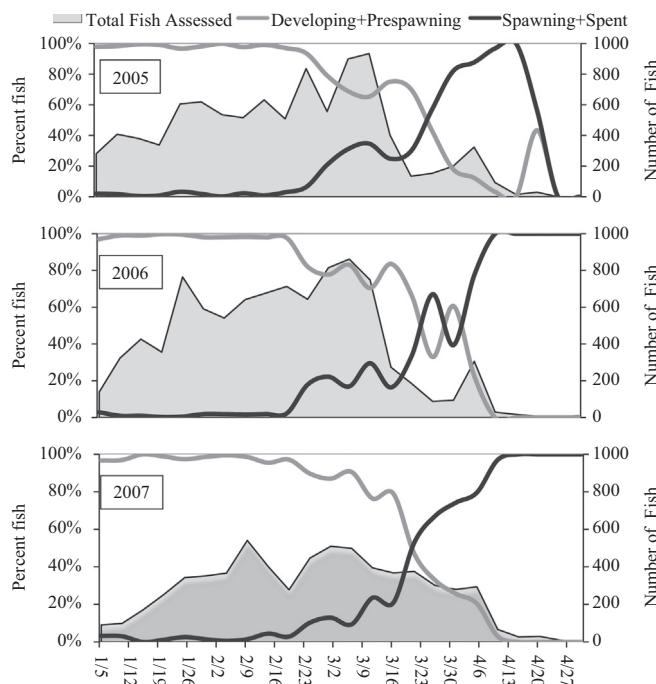
may have been reduced due to the presence, or predicted advance, of sea ice during the 2006 and 2007 spawning seasons. A decrease in fishing effort by longline vessels was reported by fishery managers

in 2007 (Hiatt et al., 2008). This decrease was likely due to the extensive sea ice coverage and may explain the lack of sampling effort and the absence of spawning stage data for this location.

**Table 3**

Calendar dates when the percentage of observer sampled fish of spawning and spent stages combined reached 20, 40–60, and 80% for each of the study years.

Year	20%	40–60%	80%
2005	March 1	March 4	April 1
2006	February 4	March 4–April 1	April 1
2007	March 2	March 3	April 1



**Fig. 6.** Spawning phenology charts for the Bering Sea and Aleutian Islands from 2005 to 2007. The left y-axis is relevant to the chart lines and represents the percent spawning stage. The right y-axis is relevant to the gray shaded areas and represents observer sampling effort over time.

Reduced sampling may have reduced the chance of encountering spawning aggregations in the northern outer shelf in 2007.

There are gear-specific differences in fish catchability which may have had minor effects on the observed distribution of Pacific cod spawning. An examination of the proportion of fish assigned to each maturity stage per gear type from late February through early March from the Unimak Pass area found that bottom trawls captured the largest percentage of fish identified as spawning stage. Fixed gear types, such as longlines and pots rely on bait to attract fish to the gear. Diet research on Pacific cod found a high occurrence of empty stomachs during spawning suggesting reduced feeding activity (Poltev et al., 2012) which may result in lower catchability of spawning stage fish by these passive gear types. Interestingly, the lowest percentage of fish identified to spawning stage was found in mid-water trawls. As a result, these patterns suggest that spawning in the northern outer shelf may be more widespread than reflected in analyses of the presence of spawning fish in commercial catches.

The comparison of visual assessments to histological evaluation of oocyte development may indicate a high level of misclassification between some stages of development. Comparisons of visual maturity to the histological examination of oocytes within ovaries is an important exercise, although differentiating between stages of yolk development at both the macroscopic and microscopic

scale can be subjective, particularly with transitioning stages of development. Aligning the markers for stage descriptions between the approaches is challenging and may account for a portion of the misclassifications (Neidetcher, 2012). Combining adjacent maturity stages for some analyses reduced the effective misclassification rates in this study. In addition, the large number of maturity assessments conducted during at-sea fishery sampling provides a robust tool for identifying the primary temporal and spatial patterns of spawning.

Despite these limitations of our study, the annual maps of the distribution of Pacific cod prespawning and spawning stages have increased our knowledge of spawning locations in the Bering Sea and Aleutian Islands. Previous conventional tagging studies describe Pacific cod spawning as large aggregations of fish over small spatial scales in areas near the shelf edge southwest of the Pribilof Islands and on the Bering Sea side of Unimak Pass, between Unimak and Unalaska Islands (Shimada and Kimura, 1994). More recently, archival tag studies have shown recoveries near the shelf edge in the vicinity of the Pribilof and Unimak Islands during the spawning season (Nichol et al., 2013). Russian trawl surveys have identified spawning and prespawning aggregations along the northern Bering Sea outer shelf, extending from Russian to US waters, in addition to areas in and around the Pribilof Islands and near Unimak Pass (Stepanenko, 1995). However, spawning activity of Pacific cod appears more widespread than suggested by those earlier surveys. Prespawning and spawning stage Pacific cod were found along the Bering Sea outer shelf (100 to 200 m depths), the shelf area between the Pribilof Islands and the slope, southeast of the Pribilof Islands closely associated with the 100 m isobath, and along the north side of Unimak Island inside of the 100 m isobath. Spawning concentrations were located near the heads of Zhemchug, Pribilof, and Bering canyons, around the shoaling isobaths of the Pribilof Islands, and among islands along the Aleutian archipelago.

#### 4.2. Oceanographic conditions by regional spawning locations

Little is known about the behavioral mechanisms driving Pacific cod aggregation patterns which may be ephemeral in nature, forming and dispersing in accordance to environmental cues. Because cod spawn weeks before larvae begin feeding, a successful strategy for cod reproduction involves the anticipation of favorable feeding conditions and transport to suitable nursery areas (Brander, 1994). We hypothesize that the geophysical and hydrological characteristics of concentrated spawning locations provide an accumulation of conditions beneficial to Pacific cod productivity. While the identified spawning concentrations were located in areas of varying topography, current structure, and water column hydrology, they may each have characteristics which would enhance survival of offspring.

The oceanographic conditions of the three areas of consistent spawning activity identified in this study provide bio-physical mechanisms that enhance primary production and possibly larval feeding. The area off the north coast of Unimak Island is subject to the influence of currents and tidal flow from the Bering Sea Canyon; this flow provides high concentrations of nutrients observed near Unimak Pass (Schumacher and Stabeno, 1998), in turn increasing productivity and improving foraging conditions for cod larvae. Around the Pribilof Islands, tidally-driven clockwise circulation (Kowalik and Stabeno, 1999) enhances entrainment of nutrient-rich deep waters from the outer shelf and Pribilof Canyon (Stabeno et al., 2008). Additionally, seasonal frontal zone which forms around the islands may enhance the retention of organisms within the “Pribilof Domain” but may also limit productivity of surface waters later in the summer (Stabeno et al., 2008).

Spawning concentrations were observed with varying occurrence over the outer shelf seaward of the Pribilof Islands between the 100 and 200 isobaths, and near the north side of St. Paul Island, and east of St. George Island. Such variations may be attributed to changing conditions as a result of variation in circulation around the islands. In the northern outer shelf, a large saline front forms along the contour of the shelf edge transecting the Pribilof and Zhemchug Canyons (Stabeno and Reed, 1994). Although on-shelf flow has been identified primarily through tidal forcing, on-shore flow associated with eddies (Stabeno and Van Meurs, 1999) is thought to provide important nutrients for high levels of primary production seen along the shelf break area (Springer et al., 1996; Stabeno et al., 1999; McRoy et al., 2001). The high level of nutrients and the hydrographic structure in these areas may provide conditions beneficial for larval cod, such as higher levels of secondary production and concentration of prey in these fronts and eddies.

Observer-assessed maturity data provide the first documentation of discrete spawning sites along the Aleutian Islands. Spawning concentrations were located between the islands and in near-shore areas on both the Bering Sea and Pacific Ocean coasts of the eastern, central, and western Aleutian Islands. These areas are dominated by tidal activity and currents flowing along the island chain and in deep passes between island groups (Stabeno et al., 2005). The dominant northward flow through the passes intersects and mixes with the Aleutian North Slope Flow bringing warm, nutrient-rich waters which drive high productivity on the northern lee sides of islands (Schumacher and Stabeno, 1998; Ladd et al., 2005). Further, this current structure may provide important local retention features or transport cod larvae onto the Bering shelf (Lanksbury et al., 2007). Where hydrological structures may isolate Bering Sea stocks from the Aleutian Island stocks, deep water passes and water conditions through the passes may deter genetic exchange along the central and western Aleutian Islands. Recent tagging experiments (Seitz et al., 2011) and genetics research (Hauser et al., 2007; Nielsen et al., 2010) have pointed toward a more complex stock structure for Pacific halibut than the previously reported single stock in the Bering Sea and Aleutian Islands. Similarly, genetic analyses of Pacific cod have identified variation between the Gulf of Alaska, the Bering Sea, and among islands in the Aleutians (Spies, 2012; Cunningham et al., 2009).

#### 4.3. Pacific cod spawning phenology

Stark (2007) found general trends in Pacific cod maturation and spawning to be seasonal and suggested that photoperiod may be the primary cue triggering reproduction in Pacific cod. These results are consistent with other studies throughout the distribution of Pacific cod. Southern stocks of Pacific cod along the west coast of North America spawn earlier than Alaska stocks. Peak spawning in the Bering Sea occurred in March during the three years of this study, consistent with observations in the Gulf of Alaska (Stark, 2007). Conversely, in Canadian stocks, peak spawning occurs in February and early March, and spawning along the west coast of the continental United States begins in December (Foucher and Westheim, 1990). Pacific cod stocks of the western Bering Sea demonstrate a similar shift in spawning phenology with later spawning along the Russian coast (Savin, 2008; Rovnina et al., 1997) than in Japanese waters (Sakurai and Hattori, 1996; Hattori et al., 1992) or off the Korean coast (Cha et al., 2007). Though the mechanisms regulating these effects are still unknown, recent studies of Atlantic cod have linked initial oocyte maturation to the autumnal equinox and the rate of oocyte maturation to ambient water temperature (Kjesbu et al., 2010).

Pacific cod maturity data presented here indicates that spawning season in the Bering Sea and Aleutian Islands begins as early as

the last week of February and extends to the first week of April, with shifts in timing of 10 days observed between the sample years. Ovary maturation was delayed in 2007 relative to 2005 and 2006 and the duration of the spawning season in 2006 was longer. Water temperatures were anomalously high in 2005, whereas 2006 was a year of transition to a colder regime and was marked with a high level of temperature fluctuation through the winter and early spring (Rodionov et al., 2007). 2007 was a cold year; the sea ice extent for that year was one of the greatest on record reaching the outer shelf, the Pribilof Islands, and the Alaska Peninsula east of Unimak Island. During high sea ice years, salinity stratification is stronger than in low sea ice years (Ladd and Stabeno, 2012). Coyle et al. (2008) suggests that years with weaker stratification are most favorable for summer production in the Bering Sea. Strong water column stratification in 2007 may have resulted in lower productivity or delayed production, and thus reduced prey resources for newly spawned cod larvae. The extended spawning observed in 2006 may have resulted from fluctuations in climate conditions during the winter months such that spawning cues varied across regions, expanding the spawning period.

#### 5. Conclusion

Gross anatomical maturity keys provide an easily implemented tool for estimating reproductive maturation in fish. The application of maturity keys by fisheries observers aboard commercial fishing vessels allowed the collection of maturity data on broad spatial and temporal scales. Pacific cod spawning activity was found to be widely distributed across the outer Bering Sea shelf and among the Islands of the Aleutian Archipelago. Within this wide distribution, discrete spawning concentrations were observed associated with island topography such as that north of Unimak Island and along the Aleutian Chain, and along the outer Bering Sea shelf in each of the study years. Because collections are possible throughout the spawning season, these data provided fishery managers with estimates of the timing and location of spawning across regions and between years. The spawning season began during late February or early March and extended through early April. Slight variations (~10 days) in the average spawning time among years may have been associated with the transition from warm to cold climate conditions during the study period. Spawning patterns provide the initial points from which patterns in stock connectivity and larval dispersal may be inferred. These data will serve as a baseline for monitoring spawning patterns over time and varying climate conditions and to identify possible shifts associated with variations in recruitment and stock abundance (Ciannelli et al., 2013).

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