Fisheries and Oceans Canada / Pêches et Océans Canada
Science / Sciences

CSAS — Canadian Science Advisory Secretariat
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Research Document 2012/032 — **Document de recherche 2012/032**

Gulf Region — **Région du Golfe**

Thorny skate (*Amblyraja radiata*) in the southern Gulf of St. Lawrence: life history, and trends from 1971 to 2010 in abundance, distribution and potential threats

Situation de la raie épineuse (*Amblyraja radiata*) dans le sud du golfe du Saint-Laurent : caractéristiques du cycle de vie, les tendances dans l'abondance et la distribution depuis 1971 à 2010, et les menaces potentielles

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ISSN 1499-3848 (Printed / Imprimé)
ISSN 1919-5044 (Online / En ligne)

Correct citation for this publication:
La présente publication doit être citée comme suit :

Swain, D.P., Benoît, H.P., Daigle, D., and Aubry, É. 2012. Thorny skate (*Amblyraja radiata*) in the southern Gulf of St. Lawrence: life history, and trends from 1971 to 2010 in abundance, distribution and potential threats. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/032. iii + 42 p.

ABSTRACT

Thorny skate (*Amblyraja radiata*) has historically been the most abundant and widespread skate in the southern Gulf of St. Lawrence. COSEWIC (the Committee on the Status of Endangered Wildlife in Canada) will be conducting an assessment of the status of this species in Canadian waters in terms of its risk of extinction. This paper presents information on life history traits, trends in the abundance and distribution of this species, and threats to its persistence in the southern Gulf of St. Lawrence. Thorny skate in the southern Gulf are fairly slow growing, with a mean length of 43.8 cm for skates ten years of age. Estimated lengths and ages at 50% maturity are 49.7 cm and 12.3 years for females and 50.5 cm and 11.9 years for males. Abundance of adult skate (skates > 50 cm in total length) in the southern Gulf has declined steadily since the beginning of the time series in 1971. The estimated decline since 1971 is 95%, and there is no indication that this decline has ceased. In contrast to the adult sizes, juvenile skates (≤ 50 cm) increased in abundance in the mid to late 1980s, were at a high level from the late 1980s to the mid 1990s and then declined sharply, followed by a sharp increase in abundance since the mid 2000s. The high abundance of juvenile skates in the early to mid 1990s and the mid to late 2000s was entirely due to high abundance of skate less than 35 cm in length. Thorny skate were widely distributed throughout the southern Gulf in the 1970s and 1980s. A striking contraction in the distribution of both juveniles and adults occurred in the 1990s and the 2000s, with distribution now largely restricted to the slope of the Laurentian Channel and northeastern regions of the Magdalen Shallows. The area occupied by mature skates in recent years is only 10% of the area occupied early in the time series. There are no directed fisheries for skates in the southern Gulf. From 1991-2010, about 96% of the total catch is estimated to have been discarded at sea. Estimated discards declined from about 400-500 t in the early 1990s to about 40 t in 2009 and 2010. In the early 1990s, most of the discards were from the cod fishery; in the 2000s, most were from the Greenland halibut fishery. The abundance of grey seals in the southern Gulf has increased over the past 40 years and may contribute to the apparent high mortality of adult thorny skate.

RÉSUMÉ

La raie épineuse a toujours été reconnu comme la raie la plus abondante et la plus répandue dans le sud du golfe du Saint-Laurent. Le COSEPAC (le comité sur la situation des espèces en péril au Canada) va évaluer le statut de cette espèce dans les eaux canadiennes afin de déterminer s'il y a risque d'extinction. Ce document présente de l'information sur les caractéristiques du cycle de vie, les tendances dans l'abondance et la distribution de cette espèce et les menaces à sa continuité dans le sud du golfe du Saint-Laurent. Les raies épineuses du sud du Golfe ont une croissance lente et une longueur moyenne de 43,8 cm pour les raies âgées de 10 ans. Les estimations des longueurs et d'âges à 50% maturité sont de 49,7 cm et 12,3 ans pour les femelles et 50,5 cm et 11,9 ans pour les mâles. L'abondance de la raie adulte (raies > 50 cm, longueur totale) dans le sud du Golfe a diminué de façon constance depuis le début de la série chronologique en 1971. La diminution, depuis 1971, est estimée à 95 % et il n'y a aucune indication que cette diminution ait cessé. Contrairement aux adultes, l'abondance des raies juvéniles (≤ 50 cm) a augmenté dans la moitié et la fin des années 1980 et était à un niveau élevé de la fin des années 1980 à la moitié des années 1990. Toutefois, elle a ensuite chuté sévèrement, mais a été suivi par une brusque augmentation depuis la moitié des années 2000. L'abondance élevé des raies juvéniles au début et à la moitié des années 1990 et à la moitié et la fin des années 2000 était entièrement due à l'abondance des raies de moins de 35 cm de longueur. Les raies épineuses étaient largement distribuées à travers le sud du Golfe dans les années 1970 et 1980. Une frappante contraction dans l'aire de distribution des raies adultes et juvéniles s'est produite dans les années 1990 et 2000. La distribution des raies épineuses est maintenant principalement limitée à la pente du chenal Laurentien et aux régions nord-est du plateau madelinien. L'aire occupée par les raies adultes dans les récentes années est seulement 10% de celle du début de la série chronologique. Il n'y a aucune pêche directe pour les raies dans le sud du Golfe. De 1996 à 2010, environ 96% des prises totales ont été considéré avoir été rejeté à la mer. L'estimation des rejets a diminué d'environ 400-500t au début des années 1990 à environ 40t en 2009 et 2010. Au début des années 1990, la majorité des rejets venait de la pêche à la morue et, dans les années 2000, la majorité provenait de la pêche au flétan atlantique. L'abondance des phoques gris dans le sud du Golfe a augmenté depuis les 40 dernières années et a peut-être contribué à la mortalité élevée des raies épineuses adultes.

INTRODUCTION

Concerns have been raised over the impact of fishing on shark and ray populations around the world (e.g., Stevens et al. 2000). Late age at maturity and slow growth make these fishes particularly vulnerable to over-exploitation (Holden 1973; Stevens et al. 2000). As predicted from these life-history characteristics, large species, such as the common skate *Dipturus batis* and the barndoor skate *D. laevis*, have been severely depleted by fishing, either locally (Brander 1981; Walker and Hislop 1998) or throughout their range (Casey and Myers 1998). However, in contrast to the larger species, the thorny skate *Amblyraja radiata* has increased in abundance in the North Sea in recent times (Heessen and Daan 1996; Walker and Heessen 1996; Walker and Hislop 1998). This species is usually discarded in North Sea fisheries (Heessen and Daan 1996; Walker and Hislop 1998), and the survival rate of discarded skates is thought to be quite high (Walker and Hislop 1998). It has been suggested that this species may have benefited from groundfisheries in the North Sea, either due to reduced interspecific competition as a result of fishery removals of large teleost fishes or due to access to large quantities of discarded fishery catch (Walker and Heessen 1996; Walker and Hislop 1998).

Thorny skate (*Amblyraja radiata*) has historically been the most abundant and widespread skate in the southern Gulf of St. Lawrence. The purpose of this paper is to provide information on life history traits and trends in the abundance and distribution of this species in the southern Gulf of St. Lawrence, in order to aid COSEWIC (the Committee on the Status of Endangered Wildlife in Canada) in its de termination of extinction-risk for this species in Canadian waters of the Northwest Atlantic. Information on potential threats is also provided. Further details can be found in Swain et al. (2005) and Swain and Benoît (2006).

BACKGROUND INFORMATION

The southern Gulf of St. Lawrence consists of a shallow shelf area, the Magdalen Shallows, with depths mostly less than 100 m, bordered by a 450-m trench, the Laurentian Channel (Fig. 1). In summer and early autumn, three water layers are present in the southern Gulf: a warm surface layer, a cold intermediate layer (the CIL, extending from about 30 to 150 m), and a warm deep layer (Gilbert and Pettigrew 1997). The CIL covers the bottom over most of the Magdalen Shallows. In winter, the southern Gulf is typically ice-covered with water temperatures near the freezing point from the surface to the bottom, except along the slope of the Laurentian Channel where the warm deep water layer covers the bottom.

Thorny skate is the most abundant of the skate species that occur in the Gulf. In summer and early autumn, thorny skate are typically widely distributed throughout the Gulf. In late autumn and early winter, they migrate into the deeper waters of the Laurentian Channel. By late November and early December, most have left waters shallower than 60 m and are concentrated along the slope of the Laurentian Channel (Clay 1991; Darbyson and Benoît 2003). By January, they are absent from waters less than 100 m (Clay 1991). In April and May they begin returning to shallower waters, with this return migration mostly complete by mid-June.

DATA SOURCES– LIFE HISTORY, DISTRIBUTION AND ABUNDANCE

Data are from annual bottom trawl surveys conducted in the southern Gulf of St. Lawrence each September since 1971. Surveys used a stratified random design, with stratification based on depth and geographic region (Fig. 1). During these surveys, trawling was conducted at 63-74 sites in each year from 1971-1983, 82-132 sites in 1984-1988, and about 140-200 sites in 1989-2010 (except 2003, when only 83 stations were successfully fished). The target fishing procedure in all years was a 30-min tow at 3.5 knots. All catches were adjusted to a standard tow of 1.75 nautical miles.

Survey coverage was expanded in 1984 to include three inshore strata (401-403). Analyses presented here are restricted to the 24 strata fished since 1971 (strata 415-439). Of these 24 strata, two (424 and 428) were not fished in 1978, while stratum 421 was not fished in 1983 and 1988. In order to maintain a consistent survey area, in the years when these strata were not fished their weights were added to those of neighboring strata in the same depth zone in calculations of stratified mean catch rates and distribution indices. For example, in 1978, half the weight associated with stratum 424 was apportioned to stratum 423 and half was apportioned to stratum 422. In 2003, no stations were fished in strata 438 and 439. In this case, predicted values for the mean catch rate in these strata were obtained using generalized linear models with terms for year and stratum. Models used a log link and assumed a Poisson error distribution allowing for overdispersion. This analysis was restricted to the 2002 – 2004 period to avoid effects of changes in distribution.

The research vessels conducting the survey were the *E. E. Prince* from 1971 to 1985, the *Lady Hammond* in 1985 to 1991, the *Alfred Needler* in 1992 to 2002, the *Wilfred Templeman* in 2003, both the *Alfred Needler* and the *Teleost* in 2004 and 2005, and the *Teleost* in 2005-2010. Tows conducted by the *E. E. Prince* used a Yankee 36 trawl; all other vessels used a Western IIA trawl. Relative fishing efficiency for thorny skate between these vessels and gears was estimated from comparative fishing experiments conducted during or shortly before the September survey in 1985, 1992, and 2004/2005. Based on the results of these experiments, catches of thorny skate were adjusted for the change in survey vessel in 1992, but no adjustments were required for the change in vessel and gear in 1985 (Benoît and Swain 2003b) or the change from the *Alfred Needler* to the *Teleost* (Benoît 2006b). No comparisons were conducted with the *Wilfred Templeman* using a Western IIA trawl.

Fishing was conducted only during daylight hours (07:00-19:00) in 1971-1984 but 24-h per day since 1985. Catches were adjusted for diel differences in fishing efficiency, as described in Benoît and Swain (2003*a*). Thorny skate had higher catchability at night than in day, and night catches were adjusted to be equivalent to day catches. These adjustments were length-dependent, with greater adjustment at smaller lengths (see Benoît and Swain 2003*a* for details). Because there were no differences in fishing efficiency for thorny skate between the *Alfred Needler* and the *Teleost* (Benoît 2006b), the diel difference in catchability for the *Teleost* was assumed to be the same as that estimated for the *Alfred Needler*.

LIFE HISTORY

Maturity has been staged for length-stratified subsamples of skate catches during the September survey since 2005. Descriptions of the maturity stages used are given in Appendix I. Fish classified as being at stages 4 and 5 were considered mature in the analyses below. Length-stratified subsamples of ageing material (thoracic vertebrae) have also been collected on these surveys. Ages were determined from vertebral band counts, following McPhie and

Campana (2009). Vertebrae were cleaned, embedded in epoxy resin and sectioned with a low-speed Isomet saw. Sections were mounted on glass slides and polished with aluminum oxide lapping film. Mounted sections were digitally photographed under reflected light, and images were then enhanced with Adobe Photoshop to improve contrast, sharpness and clarity of the growth bands. Translucent bands (winter growth) deposited along the corpus calcarium were counted by a single reader.

The maximum ages observed were 18 yr for males and 22 yr for females. Ages and lengths at 50% maturity were 11.9 yr (*N*=280) and 50.5 cm (*N*=729) for males, and 12.3 yr (*N*=303) and 49.7 cm (*N*=804) for females (Fig. 2). These results are similar to those of Templeman (1987), who reported lengths at 50% maturity of 50-56 cm for thorny skate in the Gulf of St. Lawrence. Assuming a value of 0.2 for the historical (i.e., pre-fishing) instantaneous rate of natural mortality (*M*), generation time is estimated to be 17 yr (12 + 1/0.2) for thorny skate in the southern Gulf.

Preliminary analyses of growth are shown in Figure 3. Length-at-age is similar between males and females at juvenile ages but females tend to be shorter than males at mature ages (ages 12+ yr), though data at these older ages are sparse (Fig. 3a, b). Thorny skate in the southern Gulf appear to be fairly slow growing, with a mean length of 43.8 cm for skates ten years of age (sexes combined).

Two types of models were fit to these data: von Bertalanffy models,

$$L_t = L_\infty (1 - e^{-K(t-t_o)}) \quad (1)$$

where L_t is length at age *t* years, L_∞ is the maximum theoretical length, *K* is a growth constant determining how rapidly the asymptotic length is reached and t_0 is the theoretical age at length zero; and Gompertz models,

$$L_t = L_0 e^{G(1-e^{-kt})} \quad (2)$$

where L_0 is the theoretical length at birth, *G* is the instantaneous rate of growth at age *t*, and *k* is the rate of decrease of *G*.

Von Bertalanffy models fit separately to data for males and females suggest divergent growth between the sexes at older ages (Fig. 3b). However, the parameter estimates for these models are unrealistic. For example, the estimate for L_∞ is about 20% (females) or four times (males) greater than the maximum observed length for thorny skate in the southern Gulf (88 cm, observed in the 1983 survey). Growth models fit to the data with sexes combined are shown in Figure 3c. Parameters estimated for the von Bertalanffy model are again unrealistic, with estimated L_∞ about twice the maximum observed length. Results are also shown for a “2-parameter” von Bertalanffy model with L_∞ fixed at 83.6, 95% of the maximum observed length, and for the Gompertz model. The latter model produces reasonable parameter estimates without the need to fix any parameters at assumed values. L_∞ from the Gompertz model, estimated as $L_0 e^G$, is 79.3 cm. Data from more individuals at lengths greater than 50 cm are needed to resolve growth models for thorny skate in the southern Gulf.

Figure 3d compares mean length-at-age of thorny skate in the southern Gulf to predicted lengths-at-age from a growth model for thorny skate on the eastern Scotian Shelf, taken from McPhie and Campana (2009). Unless ageing is strongly biased in one study relative to the other, this comparison indicates that length-at-age is greater on the eastern Scotian Shelf than in the southern Gulf.

CHANGES IN ABUNDANCE

Skates 51 cm and longer were assumed to be adults for this analysis, based on the estimated length at 50% maturity (about 50 cm) and given the 3-cm intervals used to record skate length in the 1970s and early 1980s (…48-50, 51-53…). Trends in relative abundance differed sharply between juvenile and adult skate (Fig. 4). Catch rates of juvenile skate fluctuated widely in the 1970s and early 1980s, but there was a general declining trend during this period. Catch rates of juvenile skate then increased in the mid to late 1980s and were at a relatively high level from the late 1980s to the mid 1990s. Juvenile abundance then declined sharply, followed by a sharp increase in abundance since the mid 2000s. In contrast, the abundance of adult skate has declined steadily since the beginning of the time series in 1971.

The decline in adult abundance over the 1971-2010 period is linear on the log scale (Fig. 5). In other words, abundance has declined exponentially over this period. The linear regression of $\log_e$ adult catch rate versus year was highly significant (P<0.0001), with a slope (b) of -0.0774. Percent decline in abundance over a period of Δt years can be estimated as $100*(1-\exp(b*\Delta t))$. Using this approach, mature abundance is estimated to have declined by 95% since 1971, a period corresponding to about 2a generations. There is no indication that this decline has ceased (Fig. 4b and 5).

The increased abundance of juvenile skate in the early to mid 1990s and the mid to late 2000s is entirely due to high abundance of skate less than 35 cm in length (Fig. 6). These increases in the abundance of small skate are surprising given the depleted spawning stock that produced them, and suggest improved survival at small sizes during these periods. The abundance of skate 40 cm and longer decreased sharply in the 1970s and the 2000s. The abundance of these larger skates has been exceedingly low throughout the 2000s. Given the relatively high abundance of smaller skates in the mid to late 1980s and throughout the 1990s, this suggests increased mortality at large sizes.

Trends in total population abundance are dominated by the variation in juvenile abundance (Fig. 7a and 4). Trends in population biomass are dominated by the variation in adult abundance (Fig. 7b and 4). Population biomass declined more or less steadily from the early 1970s to the mid 2000s and has been stable at a low level since then.

POPULATION SIZE

Fishing efficiency can be defined as the proportion of fish occurring on the grounds swept by the trawl that are actually caught and retained by the trawl. If fishing efficiency were 1, total population size could be estimated by expanding the mean catch per standard tow from the area sampled by a standard tow to the total survey area. However, fishing efficiency is not 1. It is likely that many skates in the path of the trawl escape capture. This will negatively bias this estimate (i.e., it will be an underestimate). On the other hand, the doors may herd fish into the path of the trawl. This will positively bias the estimate. Herding of skates is not likely to be strong in the survey, because skates are relatively poor swimmers and the trawl is towed at a relatively high speed during the survey (e.g., otter trawlers targeting flatfish tow at a considerably slower speed, presumably to maximize herding). Thus, “trawlable abundance” is likely to be an underestimate of the total abundance of skates.

The total survey area (strata 415-439) is 1,729,346 times the area swept between the trawl wings during a standard 1.75 nm tow. Based on the survey catch rates of adult skate standardized to daytime catchability by the *Alfred Needler* and the *Teleost*, estimates of trawlable abundance for the mature portion of the population decline from a little over a million fish in 1971-1975 to less than 62,000 fish in 2006-2010 (Table 1). Using catch rates standardized to *Lady Hammond* equivalents, with catchability adjusted to an intermediate level between day and night, estimated trawlable abundance declines from 1.9 million fish in 1971-1975 to 144,000 fish in 2006-2010 (Table 1). Trawlable biomass (all sizes) declined from about 4000 t in 1971-1975 to 300 t in 2006-2010 standardizing to daytime catchability by the *Alfred Needler*, and from about 7500 t in 1971-1975 to 1000 t in 2006-2010 standardizing to catchability by the *Lady Hammond* at the average diel level.

GEOGRAPHIC DISTRIBUTION AND HABITAT ASSOCIATIONS

METHODS

The geographic distribution of skates was mapped using the data visualization software ACON (http://www.mar.dfo-mpo.gc.ca/science/acon). Shaded contours were drawn using Delaunay triangles.

Area of occupancy (A_t) was calculated for each size class of skates in year *t* as follows:

$$A_t = \sum_{k=1}^{S} \sum_{j=1}^{N_k} \sum_{i=1}^{n_j} \frac{a_k}{N_k n_j} I \quad \text{where } I = \begin{cases} 1 \text{ if } Y_{ijkl} > 0 \\ 0 \ \text{ otherwise} \end{cases} \tag{3}$$

where N_k is the number of sites sampled in stratum *k*, *n* is the number of tows undertaken at site *j* in stratum *k*, a_k is the area of the stratum *k* and Y_{ijkl} is the catch of thorny skate in size-class *l* in tow *i* at site *j* and stratum *k*.

Area of occupancy (as defined above) will decrease as population size decreases even if there is no increase in geographic concentration (Swain and Sinclair 1994). In order to describe changes in geographic concentration, for each size class of skates we also calculated the minimum area containing 95% of skates, following Swain and Sinclair (1994). First, we calculated catch-weighted cdf's of skate catch in each year:

$$F(c) = 100 \frac{\sum_{i=1}^{n} w_i y_i I}{\sum_{i=1}^{n} w_i y_i} \quad \text{where} \quad I = \begin{cases} 1 & \text{if } \ y_i \le c \\ 0 & \text{otherwise} \end{cases} \tag{4}$$

where *c* is a level of skate catch (i.e., number per standard tow), w_i is the weighting factor for tow *i* (i.e., the proportion of the survey area in the stratum fished by tow *i* divided by the number of tows made in that stratum), *n* is the number of trawl tows in the survey, and y_i is the number of skates caught in tow *i*. *F*(c) is an estimate of the percent of skates that occur at a local density of *c* or less. We also calculated cumulative area in relation to skate catch:

$$G(c) = \sum_{i=1}^{n} \alpha_i I \quad \text{where} \quad I = \begin{cases} 1 & \text{if } y_i \le c \\ 0 & \text{otherwise} \end{cases} \tag{5}$$

where α_i is the area of the stratum fished by tow *i* divided by the number of tows made in that stratum. We evaluated *F* at intervals of 0.01, and calculated the density c_{05} corresponding to $F = 5$. $G(c)$ is the estimated area containing the most sparsely distributed 5% of skates (including areas where no skates were caught). Thus, the minimum area containing 95% of skates (D_{95}) is given by:

$$D_{95} = A_S - G(c_{05}) \tag{6}$$

where A_S is 70 075 km^2, the total survey area.

We examined variation in the habitat associations of thorny skate using cumulative distribution functions (Perry and Smith 1994) and generalized additive models (GAMs; Hastie and Tibshirani 1990). A Poisson error distribution was assumed in the GAMs, allowing for overdispersion. Models were of the form:

$$\mathrm{E}[Y_i] = \mu_i = \exp(\beta_0 + s(X_i)) \quad (7)$$

$$\mathrm{Var}[Y_i] = \phi\mu_i \quad (8)$$

where Y_i is the catch of skates in tow *i*, and $s(X_i)$ is a cubic spline function of depth. We specified the degree of smoothing for the depth term by setting its degrees of freedom to 4.

RESULTS

In the 1970s and 1980s, thorny skate were widely distributed throughout the southern Gulf, with their distribution extending into Chaleur Bay and the Shediac Valley in the western Magdalen Shallows (Fig. 8). A striking contraction in their distribution occurred in the 1990s. Thorny skate became rare in the western Magdalen Shallows, with their distribution mostly restricted to the slope of the Laurentian Channel and eastern regions of the Magdalen Shallows. A further contraction is evident in 2001-2010, when thorny skate were absent from the western Shallows and rare in southern parts of the eastern Shallows (Fig. 8). These changes in distribution were evident for both juveniles and adults (Fig. 9).

The two indices of geographic range, area occupied and D_{95}, showed parallel time trends (Fig. 10 and 11). The geographic range of juvenile skates declined throughout the 1990s and remained at a low level throughout the 2000s. The distribution of mature skates has become increasingly concentrated over the entire 40-yr time series. The area occupied by mature skates in recent years (2006-2010) is only 10% of the area occupied early in the time series (1971-1975).

A striking change in habitat associations has accompanied the recent contraction in the distribution of thorny skates in the southern Gulf. Since the early 1990s, thorny skate have occupied warmer deeper waters than in earlier years (Fig. 12). This shift in distribution does not simply reflect the local depletion (i.e., mortality) of the individuals inhabiting shallow waters, but rather a true shift in the distribution of individual skates from shallow to deep water. In conjunction with declining densities in shallow waters, densities increased in deep waters in the 1990s (Fig. 13). This may partly reflect the increased abundance of small skates during this period. However, density also increased in these deep waters for large skates (Fig. 14) even though their abundance was declining during this period.

Thorny skates do not have any known dwelling-place similar to a den or nest during any part of their life.

Changes in availability

The shift in the distribution of thorny skates toward the margin of the survey area along the slope of the Laurentian Channel raises the possibility that availability to the survey may have declined in recent years, with an increasing proportion of the stock occurring outside of the survey area in the deep waters of the Laurentian Channel. This would bias recent estimates of relative abundance downward. However, the analyses presented above on the depth distribution of thorny skate indicate that availability to the southern Gulf survey does not appear to have declined in recent years due to the shift in distribution into deeper waters. In the 1990s and 2000s, peak densities of skate occurred at depths between 150 and 250 m (Fig. 12 and 13), well inside the survey area. Densities were relatively low at depths over 300 m, suggesting that few skates occurred in the deep waters of the Laurentian Channel outside of the survey area. This was confirmed by examining the depth distribution of thorny skate in the August survey of the northern Gulf. This survey extends into the southern Gulf, covering the southern slope of the Laurentian Channel. As in the September survey, skate densities in the August survey were highest at depths between about 150 and 250 m in the 1990s and early 2000s (Fig. 15). Densities were low in the 400-500m depth zone, confirming that few skates occurred in these deep waters outside of the September survey area. However, a decline in availability due to shifts in distribution along the slope of the Laurentian Channel, either to the west into the Estuary or to the east into 4Vn, cannot be ruled out by these analyses.

Causes of the changes in skate distribution

Thorny skate, once widely distributed over the Magdalen Shallows in September, are now largely restricted to a small area in the NE corner of the Shallows and along the slope of the Laurentian Channel. Swain and Benoît (2006) examined the following hypotheses for the causes of this change in distribution: 1) an earlier offshore migration to overwintering grounds in the deep waters of the Laurentian Channel in recent years, 2) mortality of the skates that habitually occupied the now vacated habitat, 3) density-dependent habitat selection, and 4) a shift in distribution in response to the prolonged cooling of the Magdalen Shallows in the 1990s. The first two hypotheses could be rejected. A similar shift in distribution is evident in July and August catches in a bottom-trawl survey for snow crab in the southern Gulf. Thus, the disappearance of skates from the western Shallows in September surveys since the early 1990s does not seem to reflect an earlier autumn migration off the Shallows, but rather the failure for skates to move into these waters in summer. Likewise, the decline in skate densities at depths less than 100 m in the 1990s coincides with increases in densities at depths near 200 m. Thus, the change in distribution does not seem to simply reflect the local depletion (i.e., mortality) of the individuals inhabiting shallow waters, but rather a true shift in the distribution of individual skates from shallow to deep water. In contrast to these first two hypotheses, there is some evidence to support both the remaining hypotheses, as discussed below.

Variation in indices of geographic range appeared to be density-dependent rather than a response to changes in environmental conditions (Swain and Benoît 2006). In all cases, no effect of CIL temperature on D_{95} was evident once effects of skate biomass and autocorrelation were taken into account. In contrast, effects of skate biomass remained highly significant controlling for both CIL temperature and autocorrelation.

Results were more equivocal for an index tracking the shift in distribution out of the western Shallows (Swain and Benoît 2006). This index was negatively correlated with both skate biomass and CIL temperature. The shift in distribution is into a depth zone where skate condition is relatively low, contrary to the expectation for a density-dependent response. On the other hand, distribution did not shift back into shallower water when conditions warmed in the late 1990s. This may reflect a high degree of “conservatism” (Corten 2002) in skate distribution, though no conservatism is evident in the initial shift in distribution if it is proposed to be a response to cooling in the early 1990s.

Another possibility is that the shift in distribution into deeper water is a response to increased risk of predation on the Magdalen Shallows, resulting from increasing grey seal abundance. In summer, foraging by grey seals in the southern Gulf appears to be concentrated in shallower waters of the western Magdalen Shallows, based on satellite tagging of seals (Benoît et al. 2011a).

THREATS

FISHING

Background

There are no directed fisheries for skates in the southern Gulf of St. Lawrence (sGSL; Northwest Atlantic Fisheries Organization division 4T). However, skates are incidentally captured in a number of fisheries (e.g., Benoît 2006a, 2011). Though some skates are landed annually, most are discarded at sea. Skate landings are available directly from the Fisheries and Oceans Canada (DFO) landings database, termed the Zonal Interchange File Format (ZIFF) database. Discarded amounts of skates must be estimated using data collected by fisheries observers, which are deployed on a subset of commercial fishing trips (typically 5-25% of trips, depending on the fishery (Benoît and Allard 2009)) in all of the fisheries believed to catch thorny skate in the sGSL. Incidental catches of non-target species in the sGSL snow crab *(Chionoecetes opilio*) fishery are not reported by at-sea observers, though catches of fish are generally very small to nil (pers. comm. M. Lanteigne and P. Degrâce, Fisheries and Oceans Moncton). Incidental catches of skates in fisheries targeting pelagic fish such as herring (*Clupea harrengus*), mackerel (*Scomber scombrus*), and bluefin tuna (*Thunnus thynnus*) are likewise likely to be nil. The sGSL scallop (*Placopecten magellanicus*) fishery catches some winter skate (*Leucoraja ocellata*), but no thorny skate (Benoît 2011). Other important fisheries in the southern Gulf, such as the lobster (*Homarus americanus*) and rock crab (*Cancer irroratus*) fisheries, occur in waters that are too shallow to capture thorny skate.

Skates are not identified to species in the landings data, and are not consistently or reliably identified to species by the fisheries observers (Benoît 2006a). Three species of skates make up more than 99% of the skate catches in the annual September bottom-trawl survey of the sGSL (Hurlbut and Clay 1990; H. Benoît, unpublished analyses): winter skate, smooth skate (*Malacoraja senta*), and thorny skate. Fishery catches are attributed to each of these species using an empirical model.

Methods

Predicting the species composition of catches

Depth and season are strong predictors of the relative distribution of many sGSL species, including skates (e.g., Darbyson and Benoît 2003; Benoît 2006a). These variables are available along with the catch information recorded by fisheries observers, allowing species composition of fishery catches to be estimated. Furthermore, because observers report the amounts of fish that are discarded and retained, the approach described below can be used to predict species composition for both landed and discarded portions of the catches.

A multinomial regression model based on baseline-category logits (Agresti 2002, p. 267-274) has been developed and validated to model seasonal changes in the bathymetric distribution of skate species composition in the sGSL (H. Benoît, manuscript in preparation). Given that a skate has been observed, let $\pi_j(d,t) = P(Y = j \mid d,t)$ be the response probability, i.e., the probability that skate *Y* is of species *j*, given that it was caught at depth *d* (in meters) and at time *t* (day-of-year). Now define the linear model:

$$\log\frac{\pi_j(d,t)}{\pi_J(d,t)} = \beta_{0,j} + \beta_{1,j}\cdot d + \beta_{2,j}\cdot d^2 + d\cdot\sum_{p=1}^{3}\alpha_{p,j}\cdot\sin(p\omega t - \varphi_{p,j}),\quad j=1,\ldots,J\text{-}1 \qquad (9)$$

where $\omega = {}^{2\pi}\!/_{365}$ is the fundamental annual frequency, *p* defines the cycle frequency (annual, *p*=1; semi-annual, *p*=2; tri-annual, *p*=3), *J*=3 is the number of skate species in the sGSL and $\beta_{0,j}$, $\beta_{1,j}$, $\beta_{2,j}$, $\alpha_{p,j}$ (signal amplitude) and $\varphi_{p,j}$ (signal phase) are estimated parameters. The three cycle frequencies are those used to model site specific temperature changes in the sGSL (Ouellet et al. 2003), and are therefore also expected to influence species distributions. The left-hand part of eqn 9 is the logit for the response of species *j* relative to a chosen baseline species *J*. The choice of baseline species is arbitrary, because $\sum_{j=1}^{J}\pi_j(d,t) = 1$ and the *J*-1 equations defined by eqn 9 therefore determine the parameters required to define the logits of any pair of skate species (Agresti 2002, p. 268).

The multinomial harmonic regression model was fit using the maximum-likelihood method (Agresti 2002, p. 272-274) to unstandardized catches of individual skate captured in the various fishery-independent surveys carried out in the sGSL at different times of the year (Pitt et al. 1981; Hurlbut and Clay 1990; Darbyson and Benoît 2003; Savoie and Surette 2010; Bosman et al. 2011). The model in eqn 9 was found to fit the observed data well (Fig. 16). The model was also validated by fitting it to survey catches of five sGSL flatfish species and comparing the predictions to catches of these same flatfish species reported by at sea observers, who are assumed to properly and consistently identify flatfish to the species level (H. Benoît, manuscript in preparation).

For a given observed fishing set, *k*, predicted response probabilities $\hat{\pi}_{j,k}$ were obtained using the logit-transformation of eqn 9:

$$\hat{\pi}_j(d,t) = \frac{\exp(\boldsymbol{\beta}'_j\mathbf{X_k})}{\sum_{h=1}^{J}\exp(\boldsymbol{\beta}'_h\mathbf{X_k})},\quad \text{for } j=1,\ldots,J \text{ with } \boldsymbol{\beta}_J = 0 \qquad (10)$$

and where *j=J* is the baseline species and $\boldsymbol{\beta}_\mathbf{j}$ and $\mathbf{X_k}$ are shorthand for the vector of parameters for species *j* and the matrix of explanatory variables for set *k*, respectively. The expected biomass of skate species *j* in fishing set *k* was calculated as:

$$\hat{b}_{j,k} = B_k\hat{\pi}_{j,k},\ \text{with } B_k = \sum_{j=1}^{J}\hat{b}_{j,k} \qquad (11)$$

where B_k is the total biomass of skates in the catch (note that observers report catch amounts in mass only) and $b_{j,k}$ is the biomass of species *j*.

Bycatch estimation

Fourteen fisheries covering eleven commercially important taxa were the target of fishery observer surveys over the period from 1991-2010 and were used to estimate skate bycatch (Table 2). Though observer data for certain years prior to 1991 are available, the proportion of

trips covered was small and the information collected deemed not sufficiently reliable to properly estimate skate bycatch (H. Benoît, unpublished analyses).
Fisheries observers record the amounts of retained and therefore landed skates, R_k, and discarded skates, D_k, in an observed fishing set, k. These data were used to estimate total annual thorny skate bycatch as:

$$\hat{d}_{j,t} = \sum_{f}\left[\left(\frac{\sum_{k} B_{f,k,t} \cdot \hat{\pi}_{j,k}}{\sum_{k}\sum_{s} C_{s,f,k,t}}\right) \cdot \sum_{s} L_{s,f,t}\right] \quad (12)$$

where $\hat{d}_{j,t}$ is the estimated bycatch of skate species j (here thorny skate) in year t, $B_{f,k,t}$ (=$R_{f,k,t}$ +$D_{f,k,t}$) is the biomass of skate reported by observers for fishing set k in fishery f during year t, $C_{s,f,k,t}$ is the retained catch of commercial fish species s reported by observers for the set, and $L_{s,f,t}$ is the landed amount of species s in fishery f and year t taken from landings statistics contained in DFO's ZIFF database. The estimates were stratified by fishery because this is the level at which decisions on fishery observer allocations are made (Benoît and Allard 2009). Because the location, timing and fishing procedures employed all vary by fishery, stratifying in this manner also accounts for a potentially large source of variability in the relative amounts of incidentally captured and targeted species in the catch. For the fisheries observer data, fisheries were defined using the 'main species' and 'gear' variables. For the landings data, fisheries were defined using the 'species sought' variable for cases in which it was provided by the harvester and available in the ZIFF database, or the 'main species' variable otherwise, as well as the 'gear' variable. Because observer records were sparse for certain fisheries in certain years, observed sets from the fishery in adjoining years were sometimes used to calculate $\hat{d}_{j,t}$ (details in Table 2). Sparse observer records typically correspond to fisheries and years in which there was little fishing effort and few landings.

Two metrics of thorny skate bycatch were calculated using the data collected by fisheries observers: estimated landings and estimated discards. The estimated landings of thorny skate (here, species j) in year t, $\hat{r}_{j,t}$,was calculated by replacing $B_{f,k,t}$ in eqn. 12 with $R_{f,k,t}$, the amount of skate in set k in fishery f and year t that was reported as being retained by the harvester. Comparing $\sum_{j=1}^{3}\hat{r}_{j,t}$ (i.e., sum over the three sGSL skate species) with landings from the official statistics provided a validation of the bycatch estimation process. Furthermore, the estimated species composition for the retained skate catches was used to separate landings by species:

$$\hat{L}_{j,t} = L_{skate,t}\frac{\hat{r}_{j,t}}{\sum_{j=1}^{3}\hat{r}_{j,t}} \quad (13)$$

where $\hat{L}_{j,t}$ is the estimated amount of the official skate landings, $L_{skate,t}$, that is comprised of skate species j, in year t.

The amount of skate species j that was discarded in year t, was estimated by replacing $B_{f,k,t}$ in eqn. 12 with $D_{f,k,t}$, the amount of skate in set k in fishery f and year t that was reported by the observers as being discarded.

Error estimation and propagation

Uncertainty in the estimated discards was estimated using empirical bootstrapping for two key aspects of the estimation process (Efron and Tibshirani 1993). Uncertainty in the response probabilities in eqn 10 was simulated by re-sampling the data used to fit eqn 9. Survey sets were sampled with replacement from within individual surveys (and years, for multi-year surveys) and within survey strata. Strata in the sGSL are defined largely by depth (e.g., Hurlbut and Clay 1990), and stratifying the bootstrap in this way ensured that re-sampling was representative of the original temporal and depth-distribution of sets. Uncertainty associated with the estimates from eqn 9 was simulated by randomly selecting with replacement observed fishing sets within fisheries, f, and years, t. One thousand iterations were found to be sufficient to provide stable estimates of uncertainty for the discards.

Results and Discussion

Skate landings in the sGSL have varied considerably over time, peaking at around 130 tonnes in 1975 and 1976, with smaller peaks (20-60 tonnes) occurring in the late 1970s and early 1980s and during the mid to late 1990s (Fig. 17; Table 4). Landings during intervening periods, particularly 1985-1993, were relatively low. For the period over which comparisons can be made, skate landings estimated using observer records of retained catch match the official landing statistics reasonably well (Fig. 18). This helps to validate the observer data and model used to estimate skate catches, and suggests that skate discards are likely to be reliably estimated. Furthermore, this also suggests that eqn 13 might be used to accurately predict the landings for individual skate species. For thorny skate over the period 1991-2010, estimated landings peaked in the mid 1990s at around 15-40 tonnes, declining thereafter to generally ≤ 3 tonnes per year, with the exception of a second small peak in 2003-2005 (Fig. 19; Table 4).

From 1991-2010, discards comprised on average 96% (and no less than 90%) of total estimated thorny skate catches in commercial fisheries (Tables 4 and 5). Discards of thorny skate have declined from a peak of around 500 tonnes in the early 1990s to a low of around 40-50 in the late 2000s (Fig. 20). The decrease in total catches for thorny skate likely reflects in part the decline in fishing effort that has occurred in the sGSL since 1990 (Fig. 7 in Benoît and Swain 2011). Though the estimation of mean discard levels appears to be validated by the analysis in Fig. 18, it is likely that uncertainty in the estimates shown in Fig. 20 may have been under-estimated because of unrepresentative deployment of observers (Benoît and Allard 2009).

In 1991 and 1992, nearly all thorny skate discards originated from the cod mobile gear fishery (Fig. 21). From 1993-1996 most discards were in the American plaice and witch flounder mobile gear fishery. In most years since 1996, the majority of thorny skate discards has originated from fixed gear fisheries, particularly the Greenland halibut gillnet fishery during the 2000s.

Using data collected by fisheries observers on the vitality of skates just prior to discarding (Benoît et al. 2010), the mortality of sGSL skates captured and discarded in mobile gear fisheries has been estimated for two periods, the early 1990s and mid 2000s (Benoît et al. 2012). These periods differ in the intensity of fishing directed to groundfish and in the time it took harvesters to sort their catch and to discard unwanted fish, a key factor in determining whether a discarded fish will die as a result of capture and handling. During the early 1990s the survival rate of skates discarded in sGSL mobile gear fisheries was estimated at 0.51 (0.09, S.E.), while for the mid 2000s the estimated rate was 0.97 (0.02). These estimates do not incorporate indirect mortality resulting from capture and handling, such as enhanced risks of predation or disease, and should therefore be taken as minimal estimates. There are no estimates of the survival rate for skates discarded in gillnet fisheries, which have been the predominant source of capture for thorny skate during the 2000s. Short deck times associated with hauling gillnets means that skates are likely typically returned to the water rapidly, greatly enhancing discard survival potential of skates that are still alive when the nets are hauled (Benoît et al. 2010). Within-net mortality of fish has been associated with soak time and temperature, as well as the configuration of the net (Bettoli and Scholten 2006; Fréchet et al. 2006). The median soak time in the Greenland halibut gillnet fishery, which has been the main source of skate capture in recent years, is 3 days (Sylvain Ménégat, Université du Québec à Rimouski, manuscript in prep). This amount of soak time results in around 35% mortality of Greenland halibut removed from the nets. At the maximum observed soak time of 7-8 days, mortality is close to 70%. Skate survival is expected to be better because they are not vulnerable to occlusion of their spiracles by the net, in contrast to halibut which are vulnerable to operculum occlusion. The estimates for Greenland halibut might therefore serve as an upper bound for skate mortality.

The average fishery landings for the 2000s (3.9 tonnes/year) would represent between 0.4-1.3% of adult trawlable biomass, depending on whether daytime or night time catchability is assumed. During the 2000s, the mean discard estimates of 77.7 tonnes/year would have represented between 7.8-25.9% of trawlable biomass. The absence of more reliable mortality estimates for skates discarded from the Greenland halibut gillnet fishery precludes us from determining what the actual relative losses due to discarding might be.

PREDATION

The high abundance of juvenile skate in the 1990s and in recent years despite low spawner abundance suggests that mortality of juvenile skate had declined to a low level in the 1990s and 2000s. In contrast, the continuing decline in adult abundance, despite strong recruitment in the 1990s and in recent years, suggests that mortality of adult skate was at a high level in the 1990s and 2000s. Stage-structured models fit to these data confirm this expectation, indicating that juvenile mortality had declined to a low level in the 1990s and 2000s and adult mortality had increased to a high level in these decades (D. P. Swain, unpublished analyses). This pattern of declining mortality for small fish and increasing mortality for large fish is widespread throughout the marine fish community in the southern Gulf of St. Lawrence (Benoît and Swain 2008; Swain et al. 2009; Benoît and Swain 2011). An hypothesis that has been proposed to explain this widespread pattern is that small fish were released from predation when large demersal fish declined to very low levels of abundance in the 1990s due to overfishing, whereas the predation mortality experienced by large individuals increased to high levels in the 1990s due to the combination of their low abundance and the high abundance of an important predator, the grey seal (Benoît and Swain 2011; Fig. 22). Benoît et al. (2011b) reviewed existing information on the possible role of various predators (fish, birds, other marine mammals) in explaining similar mortality trends estimated for southern Gulf winter skate. They concluded that grey seals were the most likely predator of large winter skate and the most likely cause of elevated adult mortality. The evidence they reviewed is generally pertinent for thorny skate, though a detailed review is nonetheless warranted. Direct evidence for predation on thorny skate by grey seals is limited (but see Benoît and Bowen 1990), likely because consumed skates leave few hard parts (spines) in seal guts or scat. Thorny skate have however been detected in NW Atlantic grey seal diets inferred using quantitative fatty acid signature analysis (QFASA; Beck et al. 2007).

ENVIRONMENTAL CHANGE

Temperature is the only dynamic environmental variable potentially affecting thorny skate for which there is a long and continuous time series. Temperature trends in the CIL, which covers most of the Magdalen shallows, are characterized by relatively warm periods during the late 1960s and again in the late 1970s and early 1980s, and a unusually cool period during the late 1980s and much of the 1990s (Fig. 23). CIL temperatures during the 2000s have been close to average. In contrast, the deeper waters in which most thorny skate now occur warmed by close to 2^{o}C from the late 1960s to 1980 but have fluctuated without trend since 1980. While fluctuations in CIL temperature may have been involved in the shift in thorny skate distribution off of the Magdalen shallows, temperature changes are unlikely to explain changes in thorny skate mortality and abundance. Abundance has continued to decline despite stable temperatures in the Laurentian channel and average temperatures for the 2000s on the shelf.

ACKNOWLEDGEMENTS

We thank Diane Archambault (DFO, Mont-Joli) for providing data on thorny skate from the August survey of the northern Gulf of St. Lawrence.

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Table 1. Estimates of trawlable abundance (thousands) of adult thorny skates in the southern Gulf of St. Lawrence based on survey catch rates standardized to either daytime catchability by the Alfred Needler and the Teleost or to catchability by the Lady Hammond at the average diel level. The adult population is assumed to be represented by skates 51 cm or greater in total length.

	Alfred Needler day		*Lady Hammond* day/night	
Period	fish/tow	trawl. abundance	fish/tow	trawl. abundance
1971-1975	0.606	1048.314	1.117	1930.871
1976-1980	0.420	726.495	0.753	1302.254
1981-1985	0.257	443.790	0.468	810.162
1986-1990	0.212	367.470	0.424	732.814
1991-1995	0.131	226.803	0.270	467.102
1996-2000	0.109	188.225	0.258	446.435
2001-2005	0.064	109.876	0.136	234.749
2006-2010	0.036	61.654	0.083	144.198

Table 2. Commercial species and fisheries (defined by the gear class that is employed) included in the estimates of skate bycatch.

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Species	Fisheries
Atlantic cod (*Gadus morhua*)	Fixed and mobile gear
Redfish (*Sebastes sp.*)	Mobile gear
Atlantic halibut (*Hippoglossus hippoglossus*)	Fixed gear
Greenland halibut (*Reinhardtius hippoglossoides*)	Fixed gear
White hake (*Urophycis tenuis*)	Fixed and mobile gear
American plaice (*Hippoglossoides platessoides*)	Fixed gear
American plaice and witch flounder (*Glyptocephalus cynoglossus*)	Mobile gear
Winter flounder (*Pseudopleuronectes americanus*)	Fixed and mobile gear
Yellowtail flounder (*Limanda ferruginea*)	Mobile gear
Spiny dogfish (*Squalus acanthias*)	Fixed gear
Shrimp (*Pandalus* sp.)	Mobile gear

Table 3. Summary of the fisheries and years for which estimates of bycatch are based on multiple years of pooled fisheries observer data. The years for which the data were pooled for the estimation are also indicated. For fisheries and years not listed here, relevant within-year data were used.

Fishery	Years for which pooled data were used	Years included in the pooled data
Cod (fixed gear)	1991	1991-1993
	1993-1997	1991-1999
Dogfish	1991, 1992	1993-1995
	2000-2006	1998-2006
Halibut	1991-1993, 1996, 1997	1991-1999
American plaice (fixed gear)	1991-1993, 1998-2007	1991-2010
Redfish	1998,1999	1991-1999
	2000-2010	2000-2010
Greenland halibut	1992	1991-1994
Winter flounder (fixed gear)	1991-2010	1991-2010
Winter flounder (mobile gear)	2006-2010	2000-2010
White hake	1991-1995	1991-1995
Yellowtail flounder	1991-1998	1995-1998
	1999-2002	2000-2005

Table 4. Official skate landings for 1971-2010 and estimated landings (with lower and upper 95% confidence intervals, LCI and UCI respectively) for southern Gulf of St. Lawrence thorny skate (1991-2010). All values are in tonnes.

		Estimated		
Year	Landings	Mean	LCI	UCI
1971	8.00			
1972	2.00			
1973	3.00			
1974	132.00			
1975	131.00			
1976	43.00			
1977	5.00			
1978	12.00			
1979	17.00			
1980	22.00			
1981	66.00			
1982	1.00			
1983	35.00			
1984	0.00			
1985	0.00			
1986	3.00			
1987	0.00			
1988	1.00			
1989	1.00			
1990	0.68			
1991	4.19	2.30	0.78	5.24
1992	1.66	0.87	0.26	2.09
1993	7.98	4.53	2.01	9.48
1994	55.83	38.47	1.41	96.50
1995	32.74	20.62	10.07	37.54
1996	24.36	15.16	2.10	31.96
1997	9.55	4.85	0.85	11.24
1998	8.04	4.05	0.77	10.40
1999	11.17	7.68	1.26	15.92
2000	5.68	2.07	0.24	8.59
2001	3.61	2.03	0.21	4.13
2002	6.25	3.49	1.03	5.87
2003	9.86	5.87	2.34	11.22
2004	21.02	11.15	3.80	22.04
2005	13.88	7.98	1.18	20.65
2006	2.82	1.28	0.38	2.76
2007	1.85	1.44	0.05	3.65
2008	1.92	1.16	0.27	2.54
2009	5.32	2.74	0.16	7.52
2010	3.27	1.22	0.32	2.76

Table 5. Estimated discards (in tonnes, with lower and upper 95% confidence intervals, LCI and UCI respectively) for southern Gulf of St. Lawrence smooth and thorny skate (1991-2010).

Year	Mean	LCI	UCI
1991	406.93	303.79	526.62
1992	573.34	460.66	690.82
1993	212.28	144.19	332.63
1994	499.38	306.22	666.01
1995	259.42	164.98	399.44
1996	198.20	135.49	287.31
1997	252.31	154.17	408.11
1998	239.73	172.67	319.34
1999	214.20	173.02	280.05
2000	166.92	129.69	215.75
2001	91.83	68.96	121.74
2002	55.43	44.10	71.94
2003	55.09	45.62	67.07
2004	98.94	66.15	139.99
2005	93.79	69.77	126.68
2006	80.44	62.47	106.72
2007	54.30	31.64	79.30
2008	80.27	47.91	120.13
2009	41.28	28.83	55.88
2010	41.75	27.79	62.61

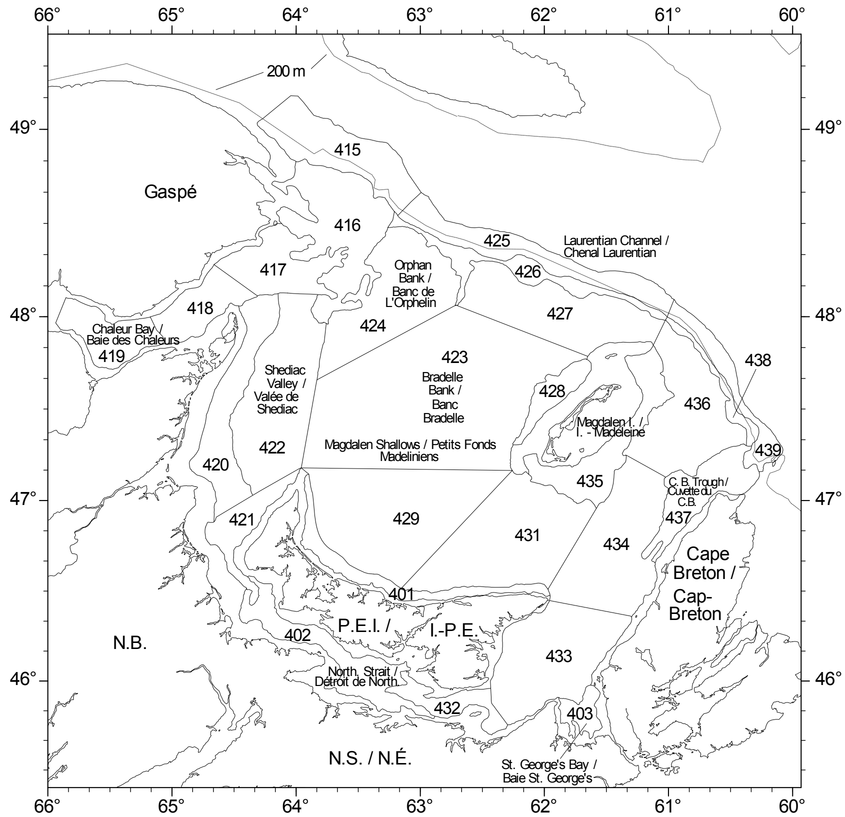

Figure 1. The southern Gulf of St. Lawrence, showing the strata used in the annual September bottom-trawl survey.

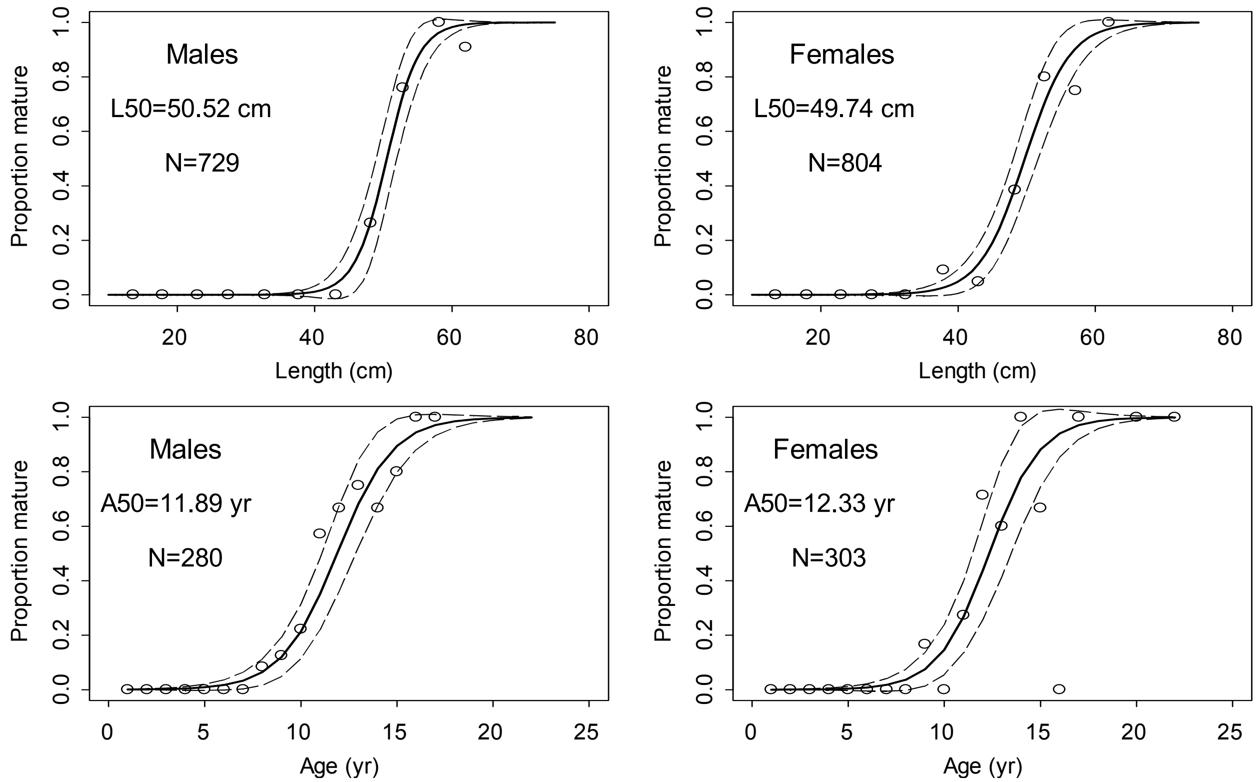

Figure 2. Age and length at maturity for thorny skate in the southern Gulf of St. Lawrence, 2005-2009. Note that the outlying point at age 16 in the bottom right panel is based on 1 fish.

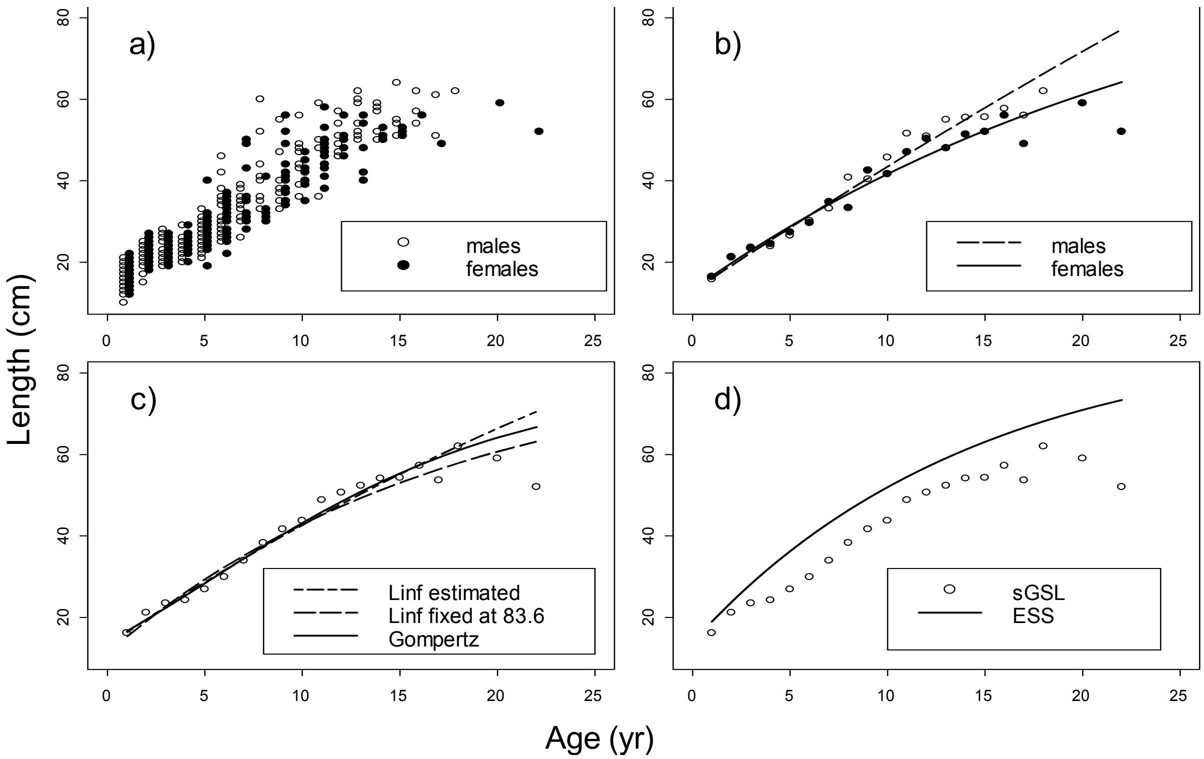

Figure 3. Length-at-age of thorny skate in the southern Gulf of St. Lawrence, 2005-2007: a) individual skate; observations offset by 0.15 (females) or -0.15 (males) years, b) mean length-at-age for males (open circles) and females (closed circles); lines show predicted length-at-age from von Bertalanffy models fit to the individual observations, c) mean length-at-age and model predictions with sexes combined, d) southern Gulf data compared to predictions of a model fit to data from the eastern Scotian Shelf (from McPhie and Campana 2009).

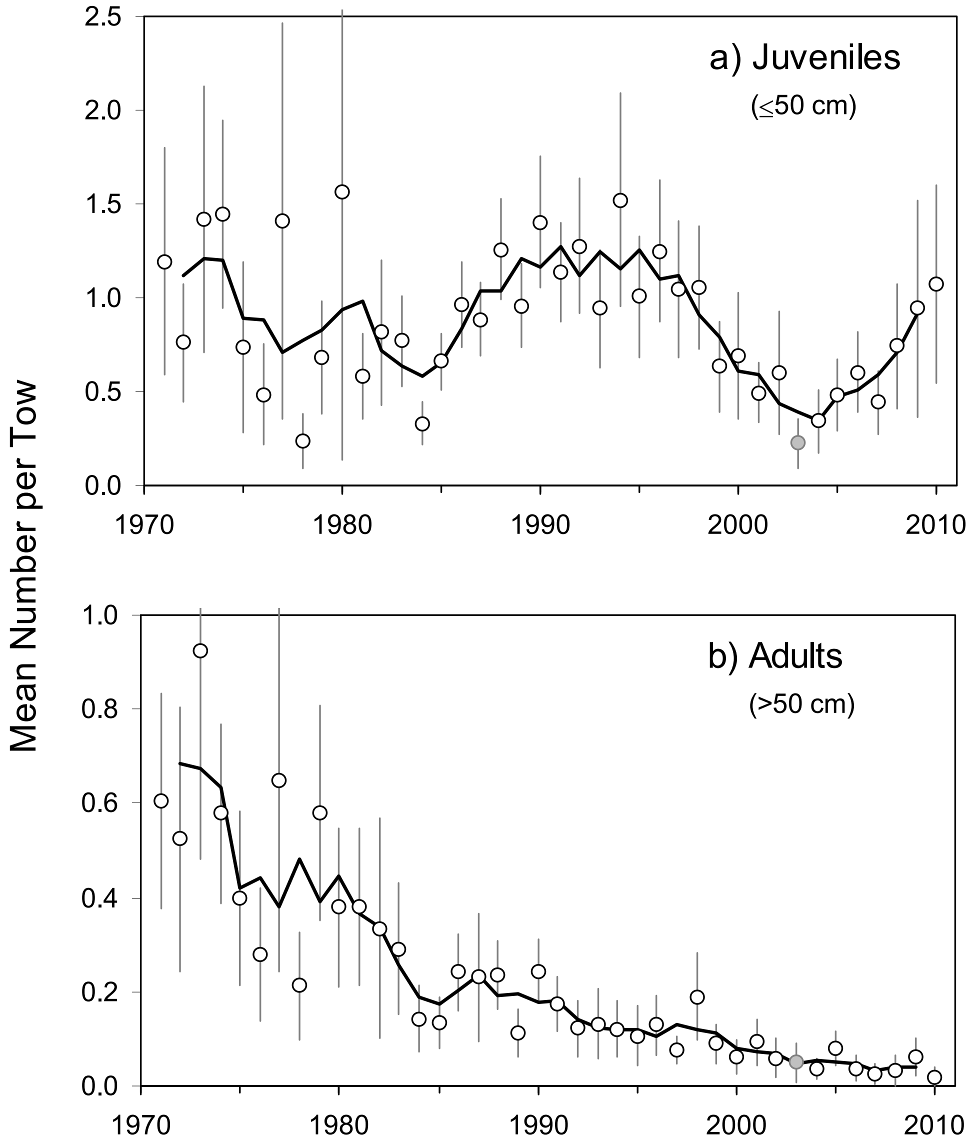

Figure 4. Stratified mean catch rates of thorny skate in the September survey of the southern Gulf of St. Lawrence. Vertical lines are ±2SE. Heavy lines show 3-yr moving averages. Catch rates are adjusted to daytime catchability by the Alfred Needler. The grey circles denote the catch rates from 2003 survey, which was conducted by an uncalibrated vessel (the Wilfred Templeman*).*

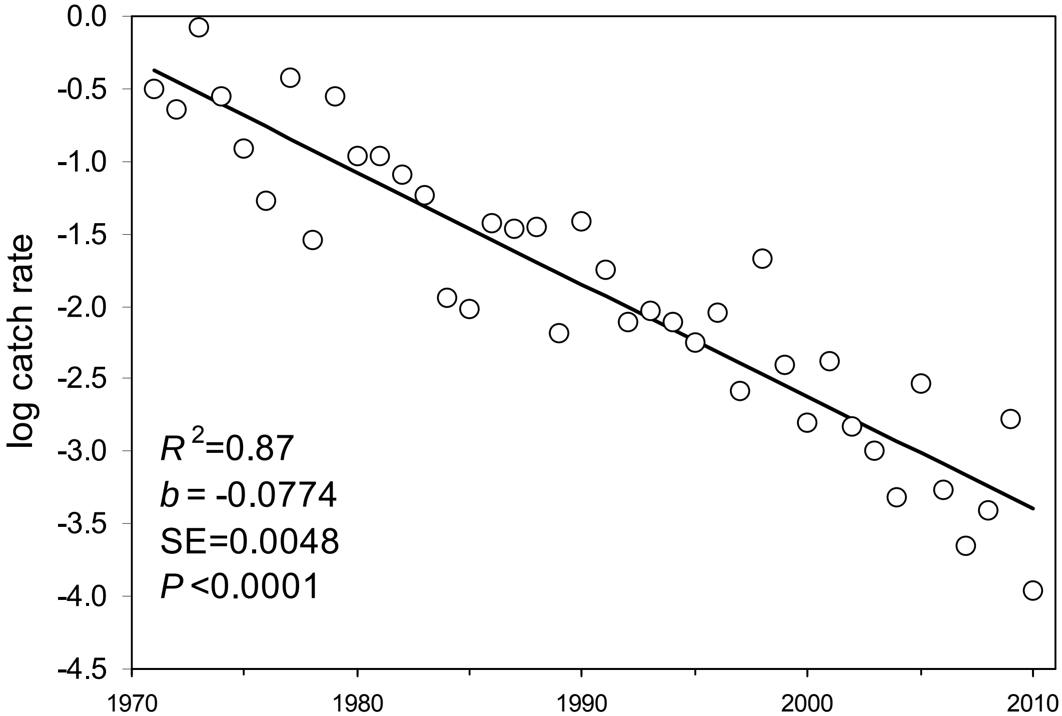

Figure 5. Log$_e$ – transformed catch rates of adult (>50 cm TL) thorny skate in September surveys of the southern Gulf of St. Lawrence. Line shows the regression of log$_e$ catch rate on year.

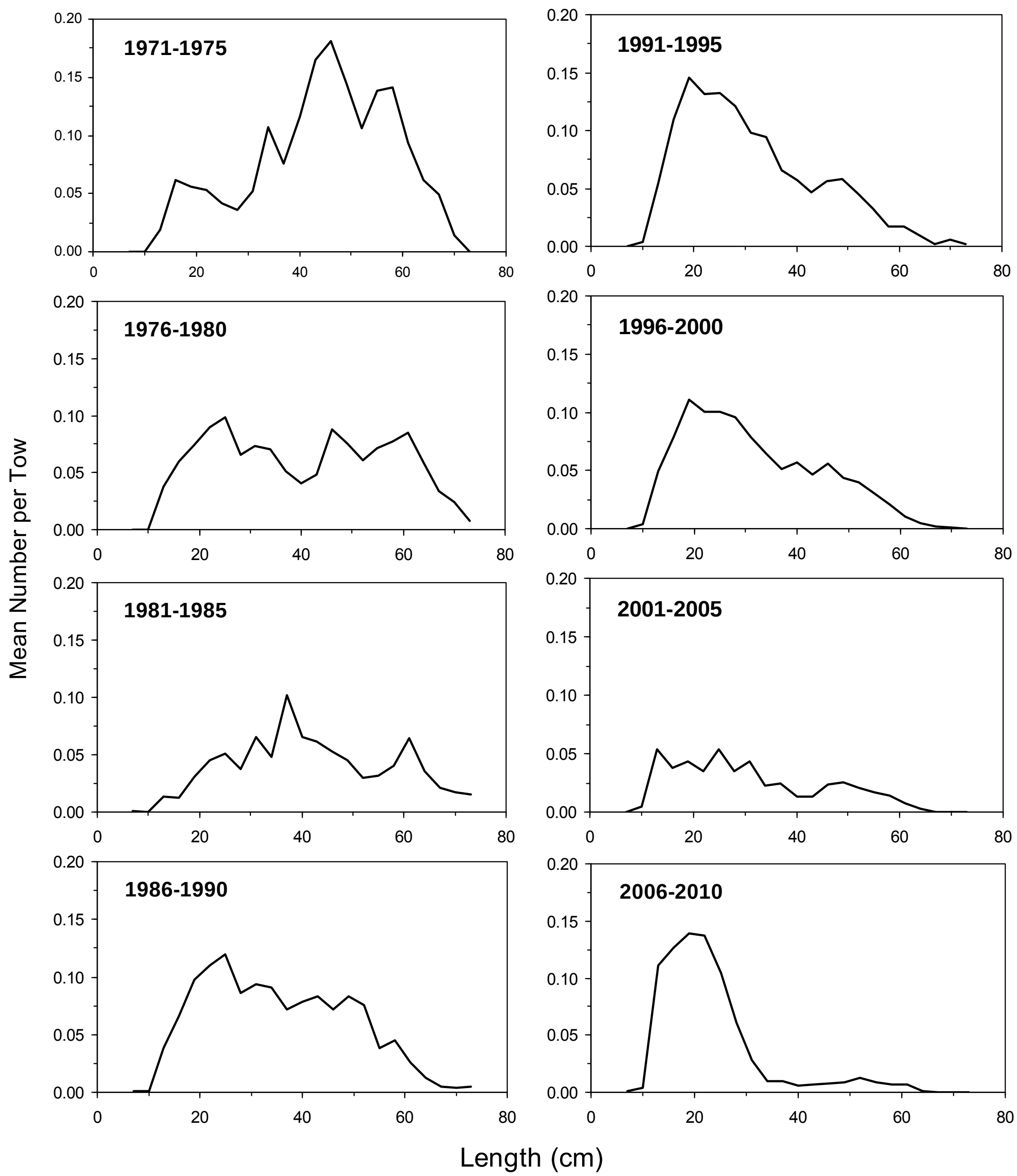

Figure 6. Stratified mean length frequency distributions of thorny skate in the southern Gulf of St. Lawrence in September in 5-yr blocks.

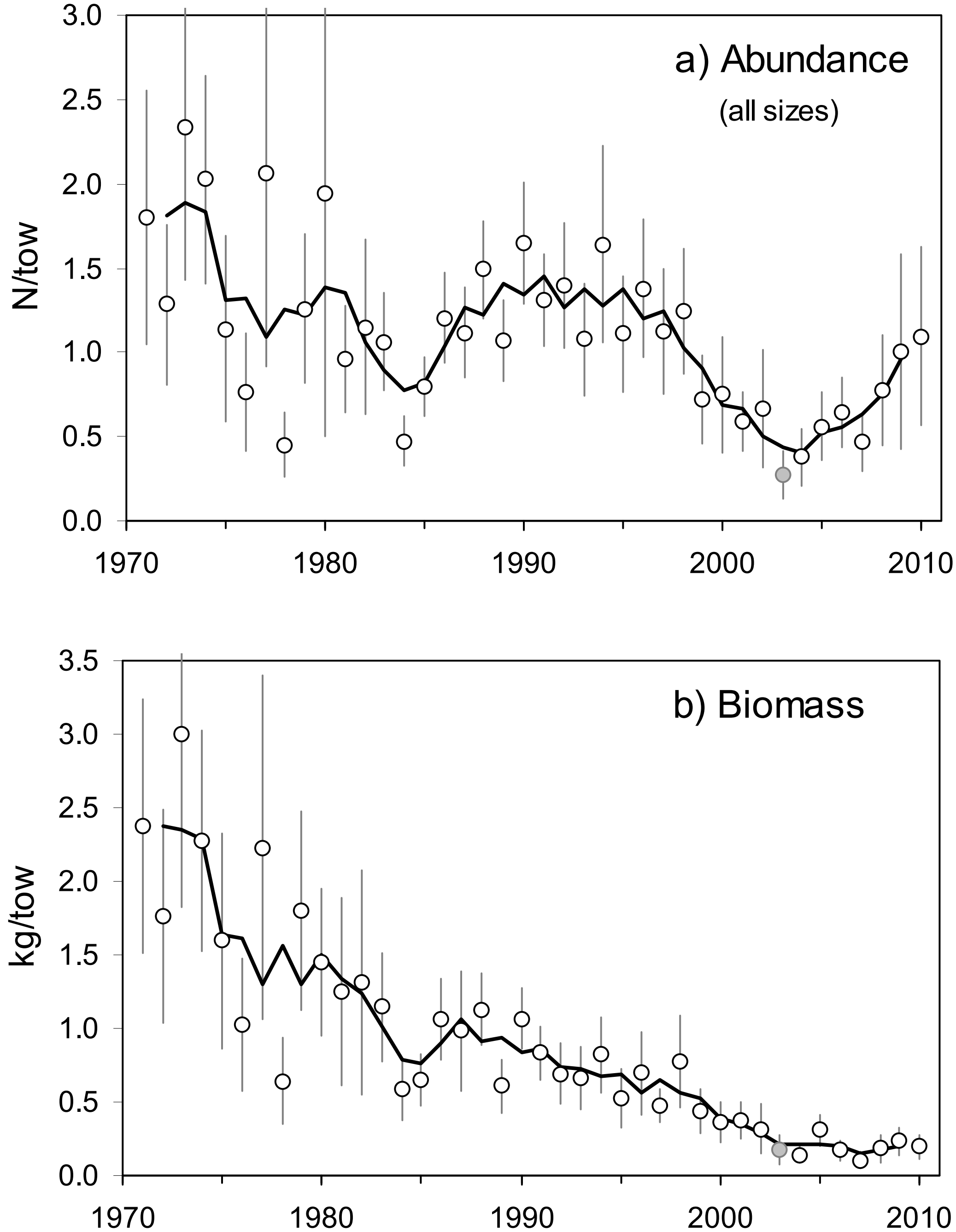

Figure 7. Stratified mean catch rates of thorny skate (all sizes) in the September survey of the southern Gulf of St. Lawrence. Vertical lines are ±2SE. Heavy lines show 3-yr moving averages. Catch rates are adjusted to daytime catchability by the Alfred Needler. The grey circles denote the catch rates from 2003 survey, which was conducted by an uncalibrated vessel (the Wilfred Templeman*).*

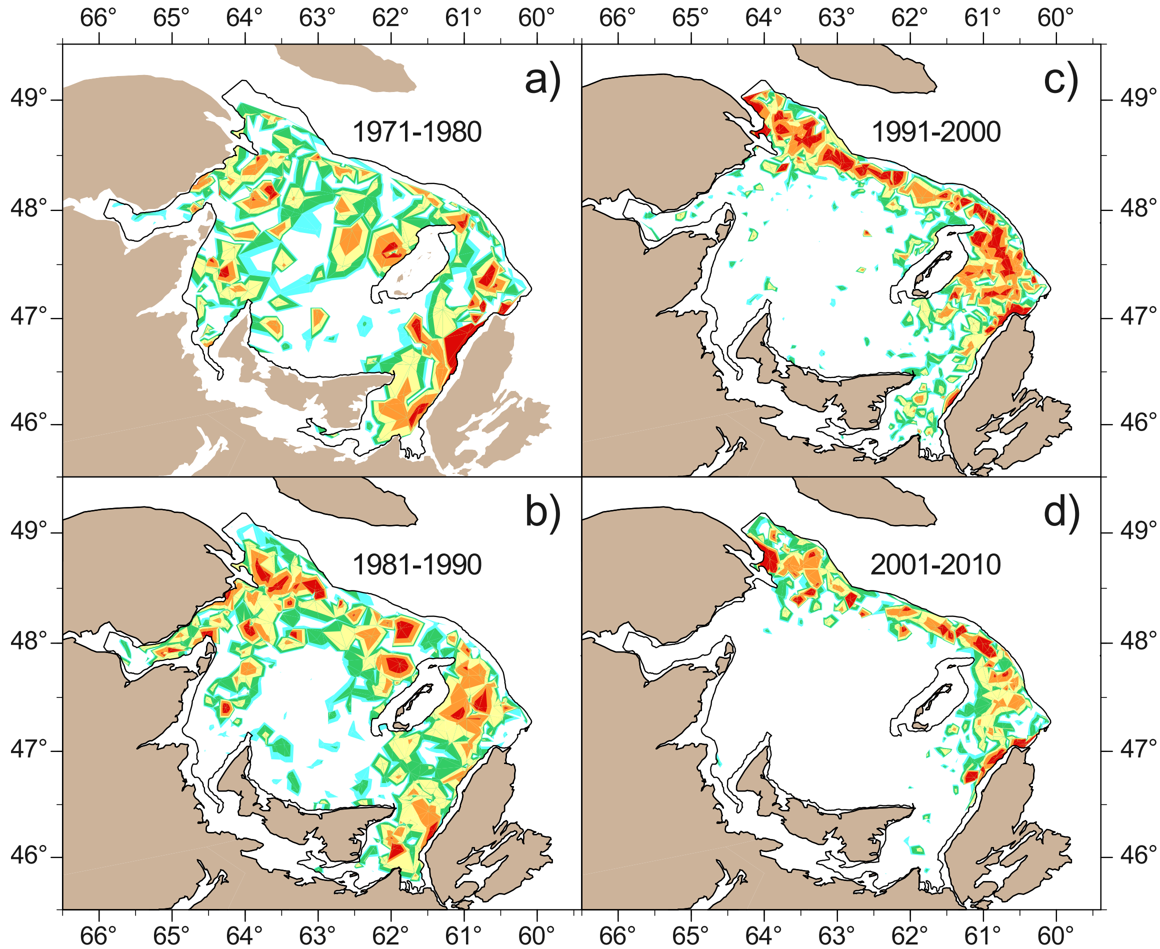

Figure 8. Geographic distribution of thorny skate catches in the September survey of the southern Gulf of St. Lawrence. Contour intervals are the 10th (blue), 25th (green), 50th (yellow), 75th (orange) and 90th (red) percentiles of nonzero catches (fish/tow) over the 1971-2010 period.

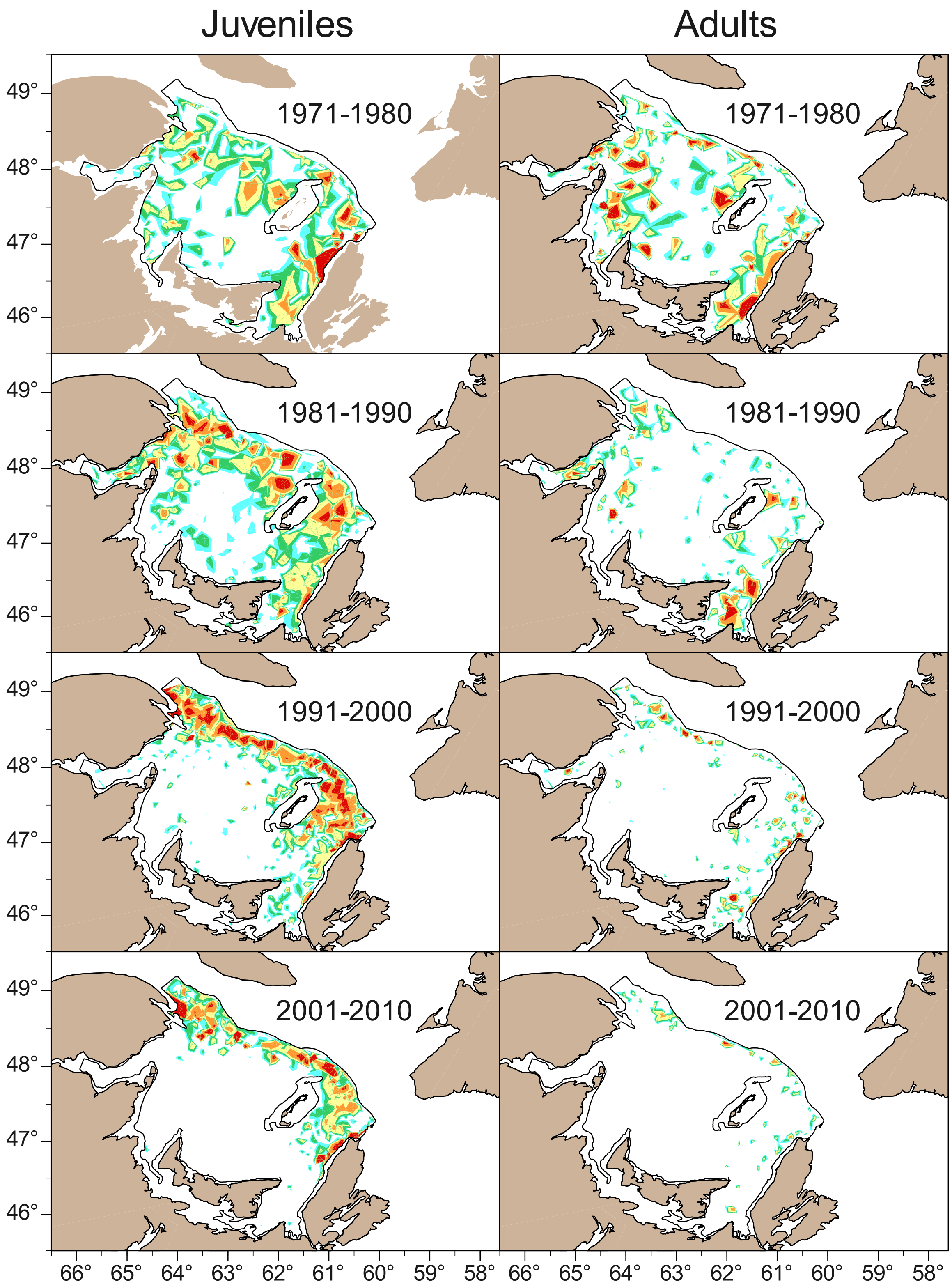

Figure 9. Geographic distribution of juvenile and adult thorny skate catches in the September survey of the southern Gulf of St. Lawrence. Contour intervals are the 10th (blue), 25th (green), 50th (yellow), 75th (orange) and 90th (red) percentiles of nonzero catches (fish/tow).

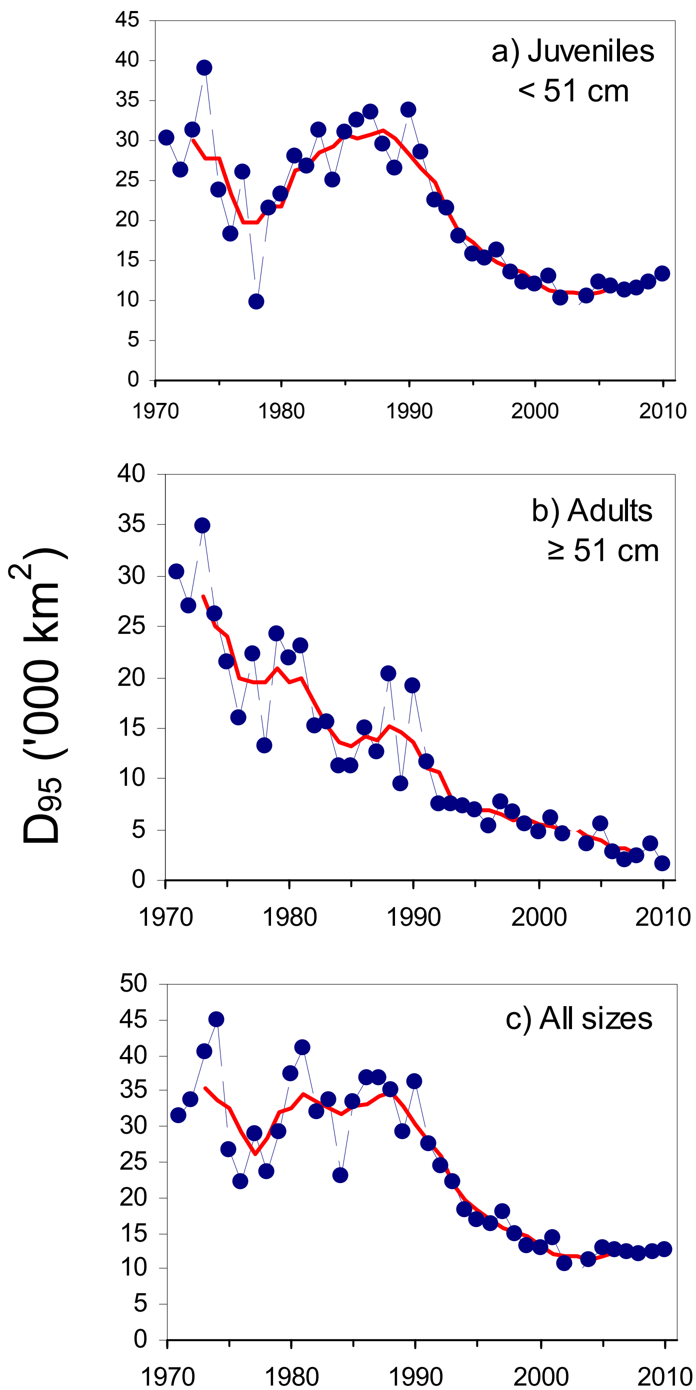

Figure 10. Time trend in an index of geographic range (D95) for three size classes of thorny skate in September in the southern Gulf of St. Lawrence. Heavy line is a 5-yr moving average.

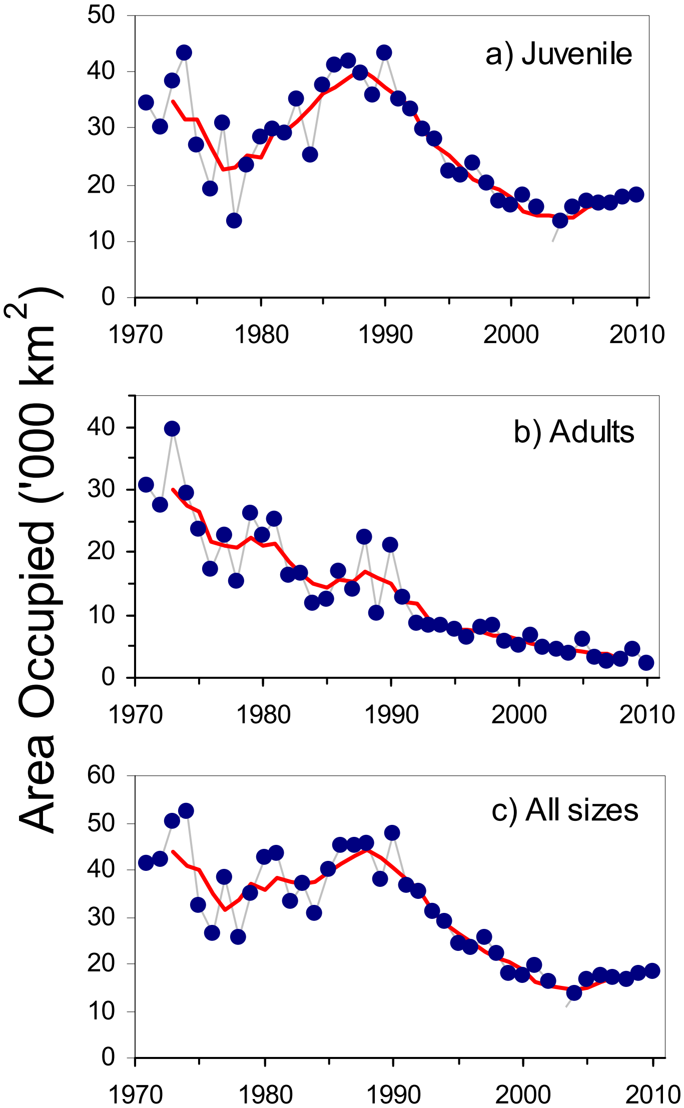

Figure 11: Area occupied by three size classes of thorny skate in September in the southern Gulf of St. Lawrence, 1971-2010. Heavy line is a 5-yr moving average.

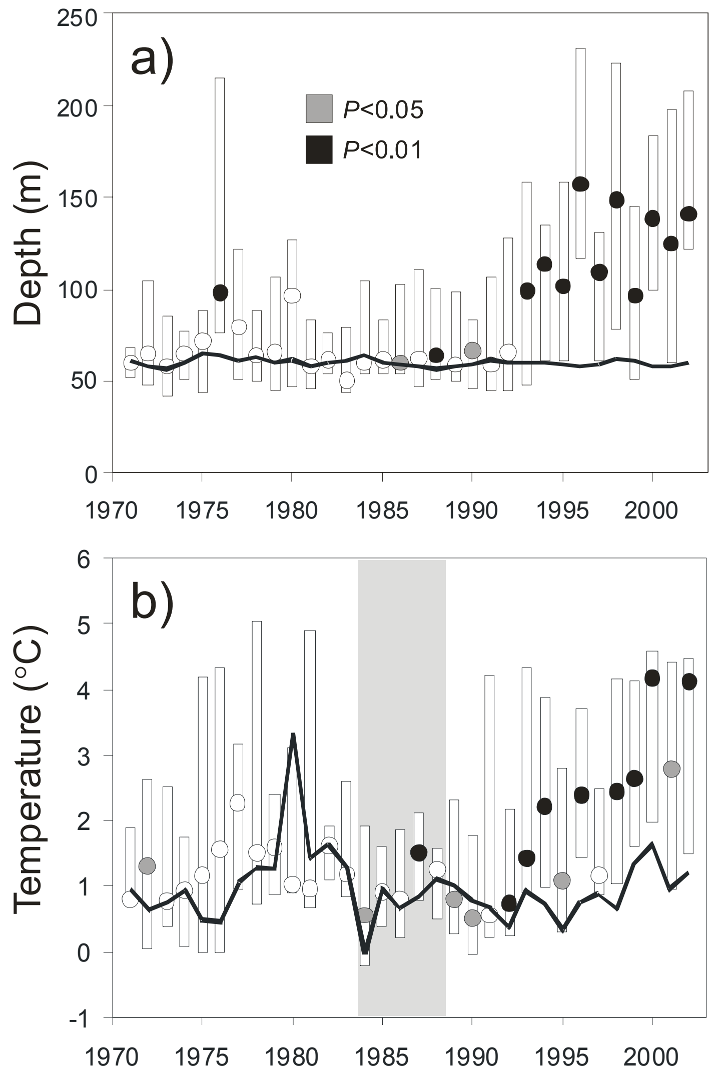

Figure 12. Associations of thorny skate with a) depth and b) temperature in September in the southern Gulf of St. Lawrence. Line shows the median depth or temperature available in the sampled area. Circles show the median depth or temperature occupied by thorny skate. Bars show the 25th to 75th percentiles of occupied depths or temperatures. Shaded circles indicate a statistically significant association between skates and depth or temperature. Near-bottom temperatures were not available for depths greater than 155 m in the shaded years in panel b (1984-1988). See Swain and Benoît (2006) for further details.

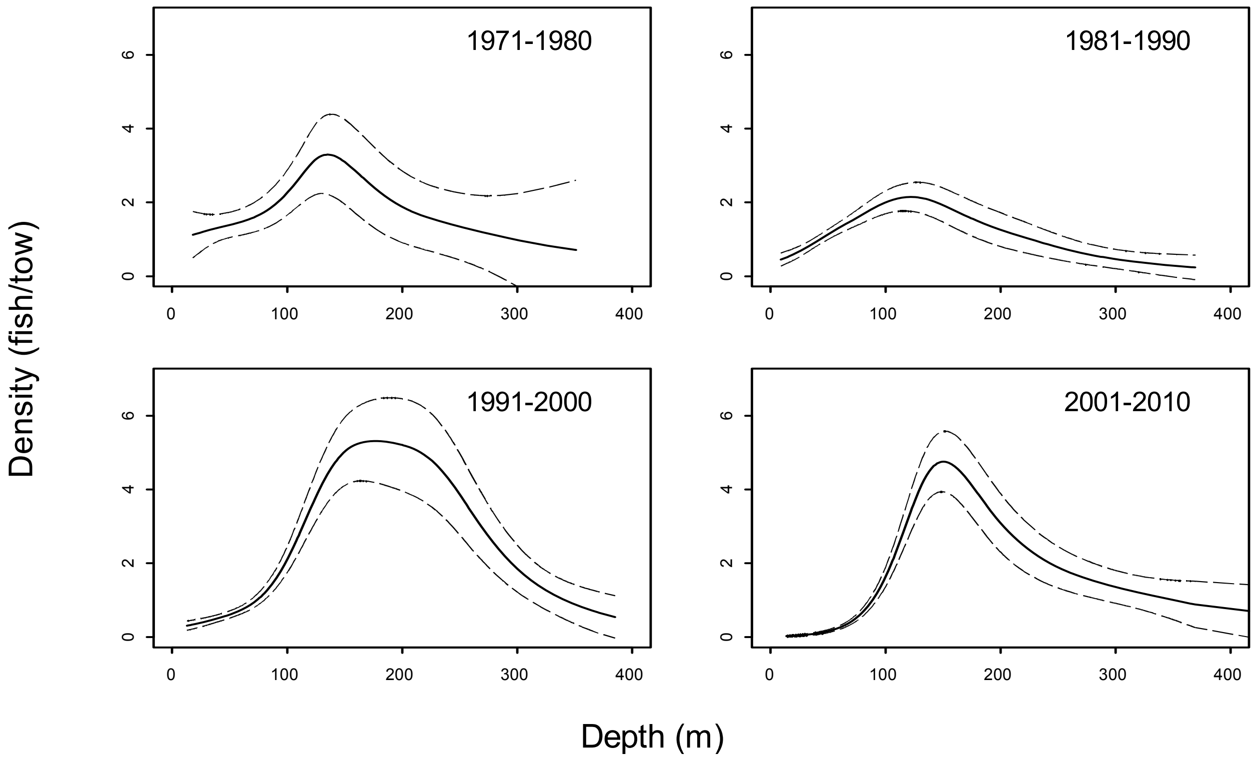

Figure 13. Effect of depth on the local density of thorny skate in the southern Gulf of St. Lawrence in September. Solid line is the predicted density and dashed lines are ± 2SE.

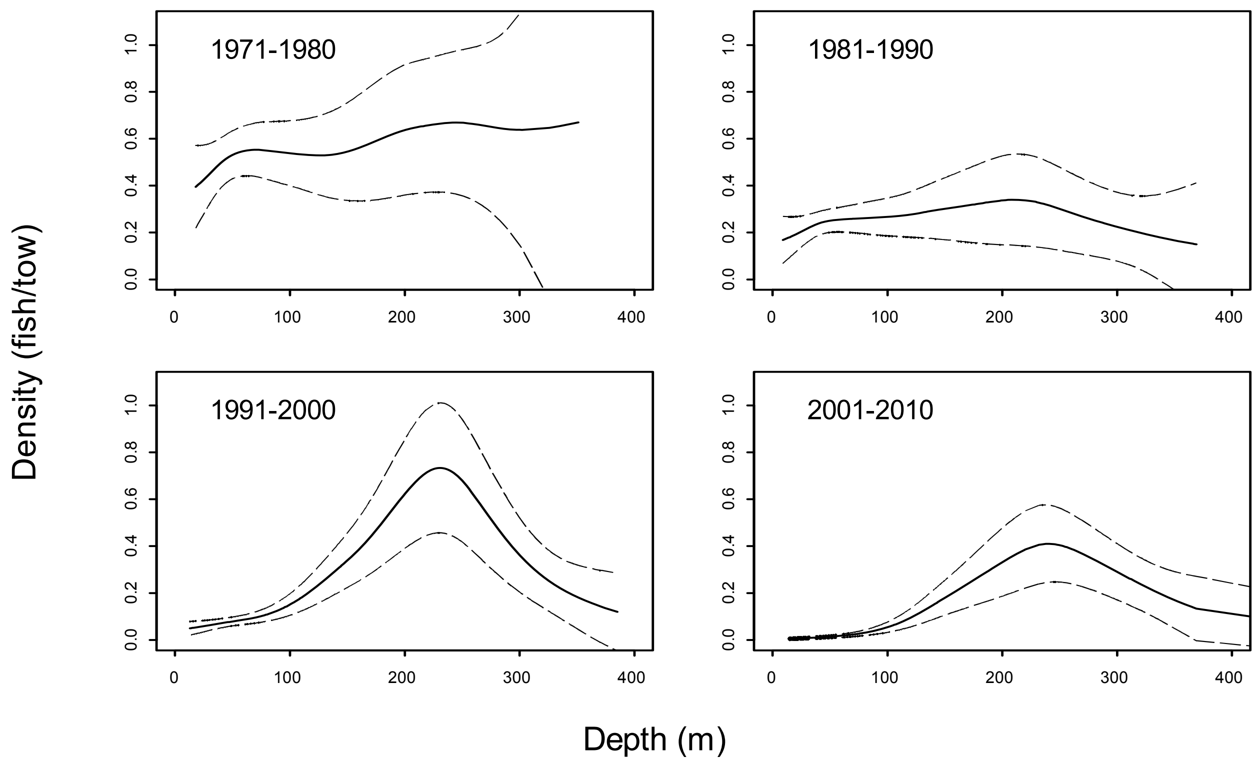

Figure 14. Effect of depth on the local density of adult thorny skate in the southern Gulf of St. Lawrence in September. Solid line is the predicted density and dashed lines are ±2SE.

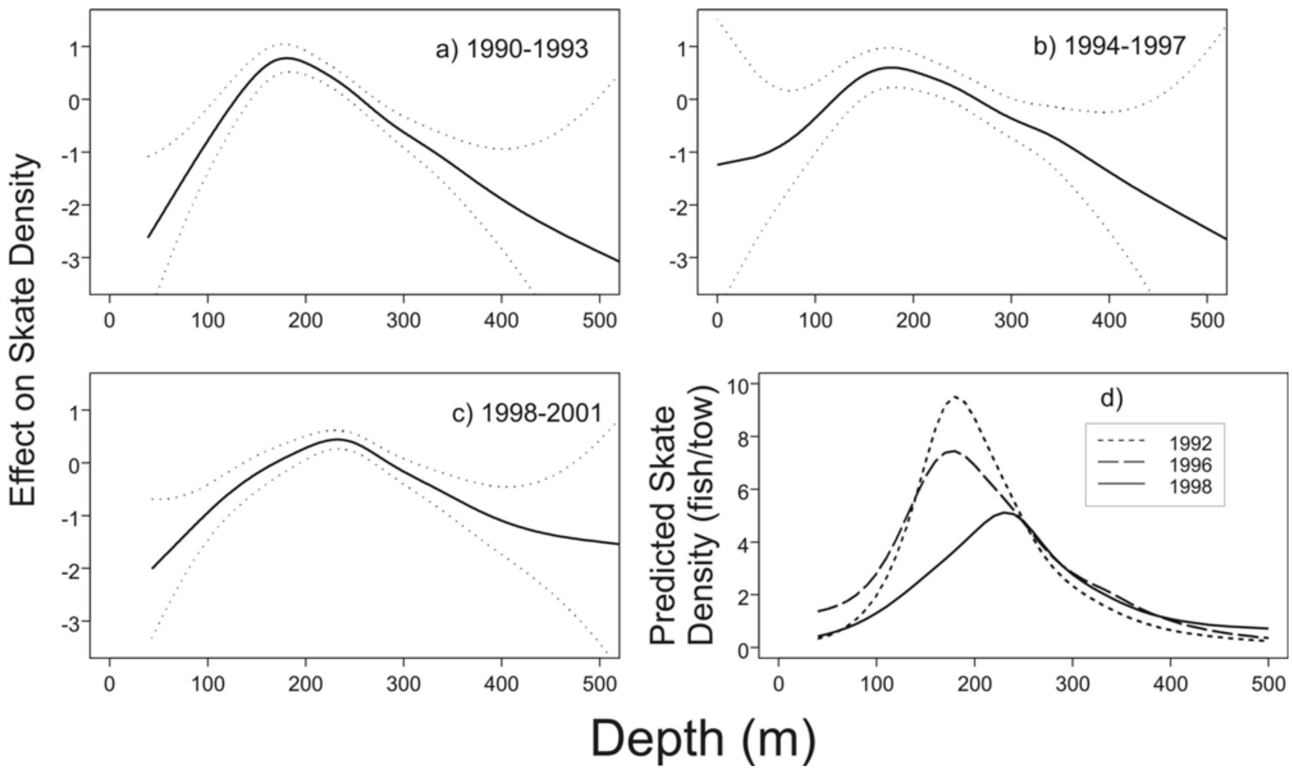

Figure 15. Effect of depth on the local density of thorny skates (all sizes) in the August survey of the northern Gulf of St. Lawrence. Panels a-c: effect of depth (on a $\log_e$ scale) on skate density for three time periods. Solid line shows the predicted relationship, and the dotted lines are ±2SE. Note that models included an effect of year not shown in these panels. Panel d: predicted density of thorny skate for a selected year in each time period. Density in the selected year was near the average for the period.

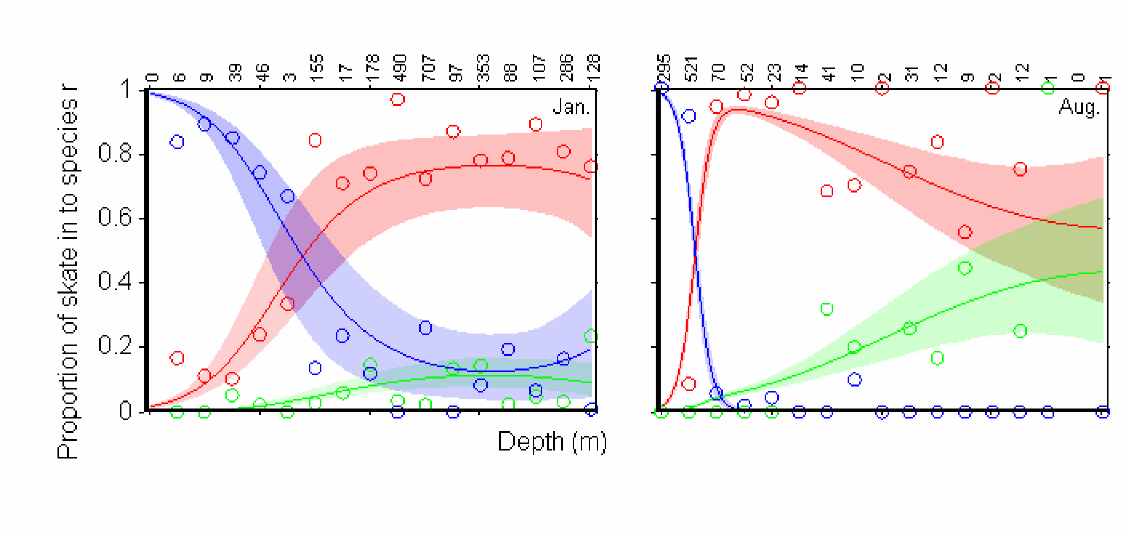

Figure 16. Examples of the fit of the multinomial harmonic regression model for two months, January (left panel) and August (right). Observed (circles) and predicted (lines, with the 95% confidence band denoted by shading) relative proportions of the three sGSL skate species (thorny skate, red; smooth skate, green; winter skate, blue) are shown as a function of depth. Survey catches were summarized in depth bins of 25 m for plotting. The numbers above each panel indicate the number of individual skate from a particular depth and time bin that were used to fit the model.

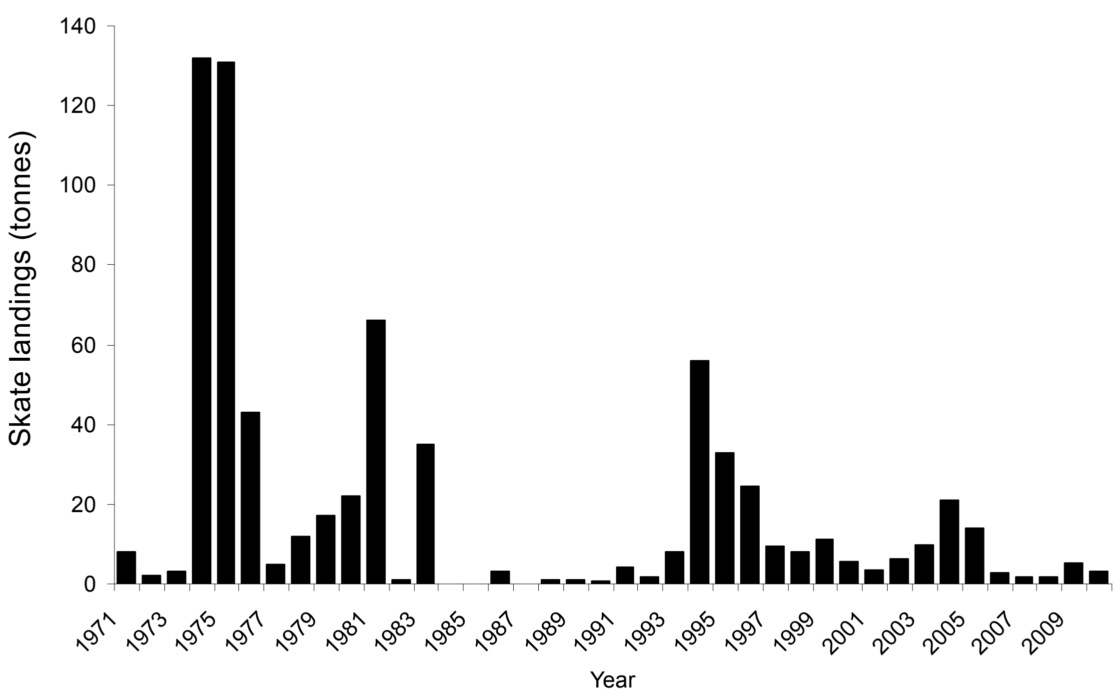

Figure 17. Landings of skates in the southern Gulf of St. Lawrence (NAFO Div. 4T), 1971-2010.

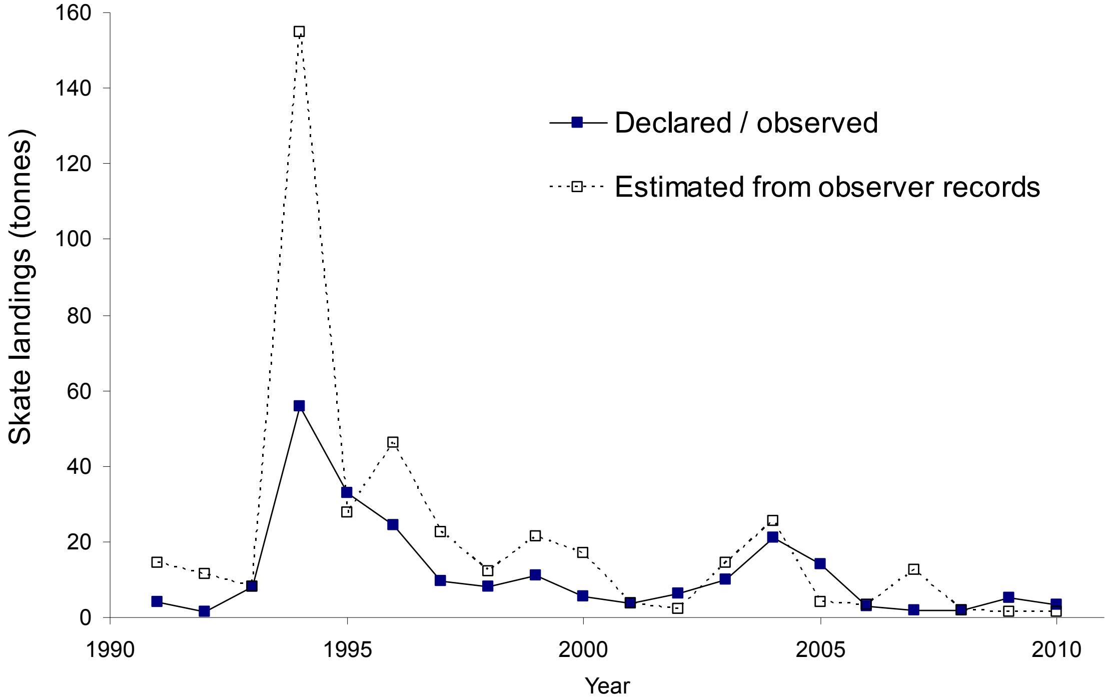

Figure 18. Official landings of skates (based on declared catches or dockside catch observation) and landings estimated using the amount of retained skates reported by fisheries observers.

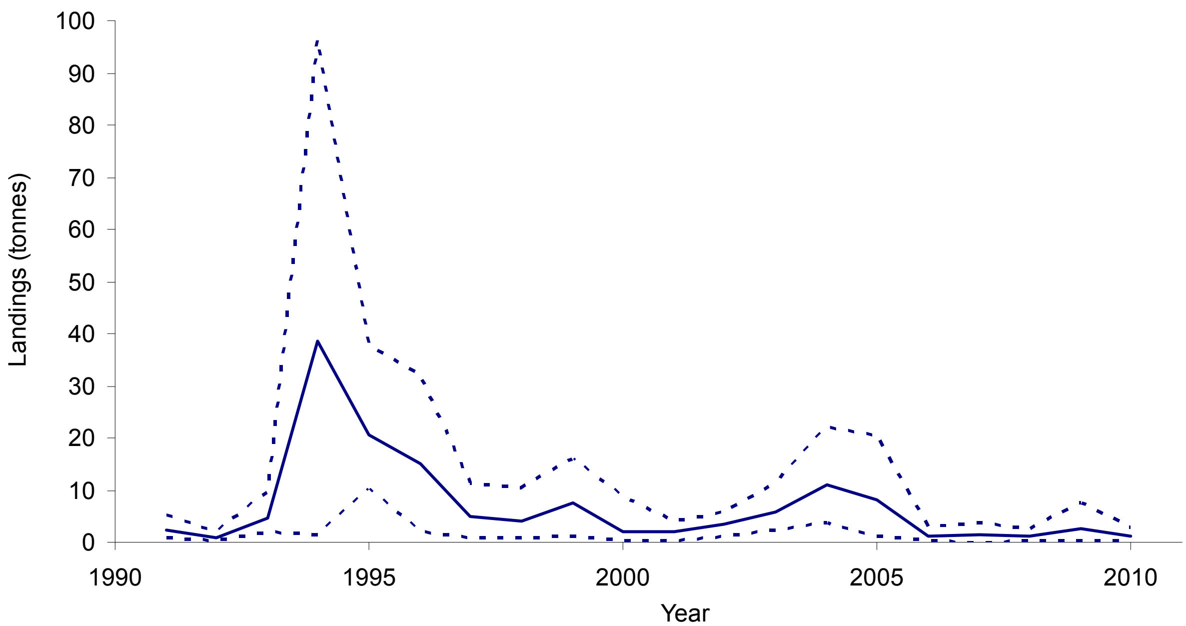

Figure 19. Estimated landings of thorny skate based on the multinomial harmonic regression model (with 95% confidence interval indicated by the dashed lines), 1991-2010.

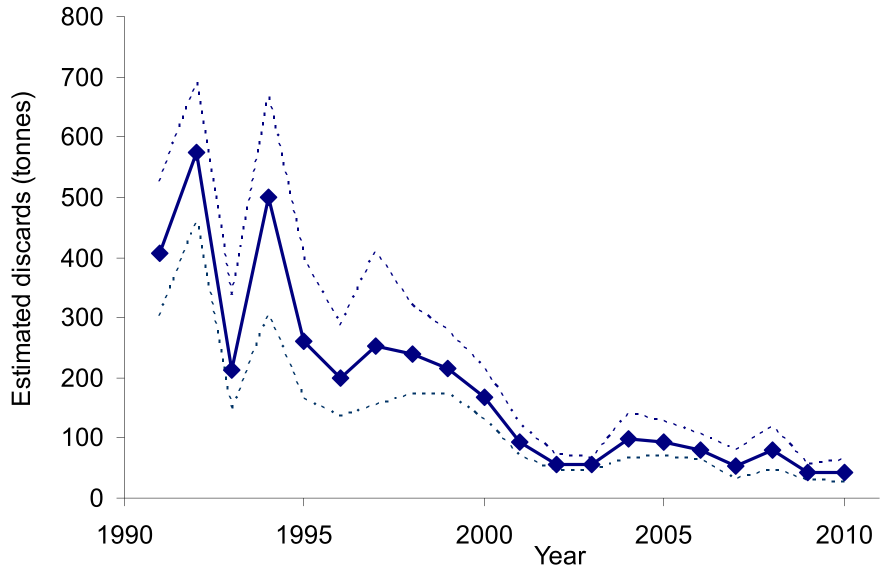

Figure 20. Estimated discards of thorny skate (with 95% confidence interval indicated by the dashed lines), 1991-2010.

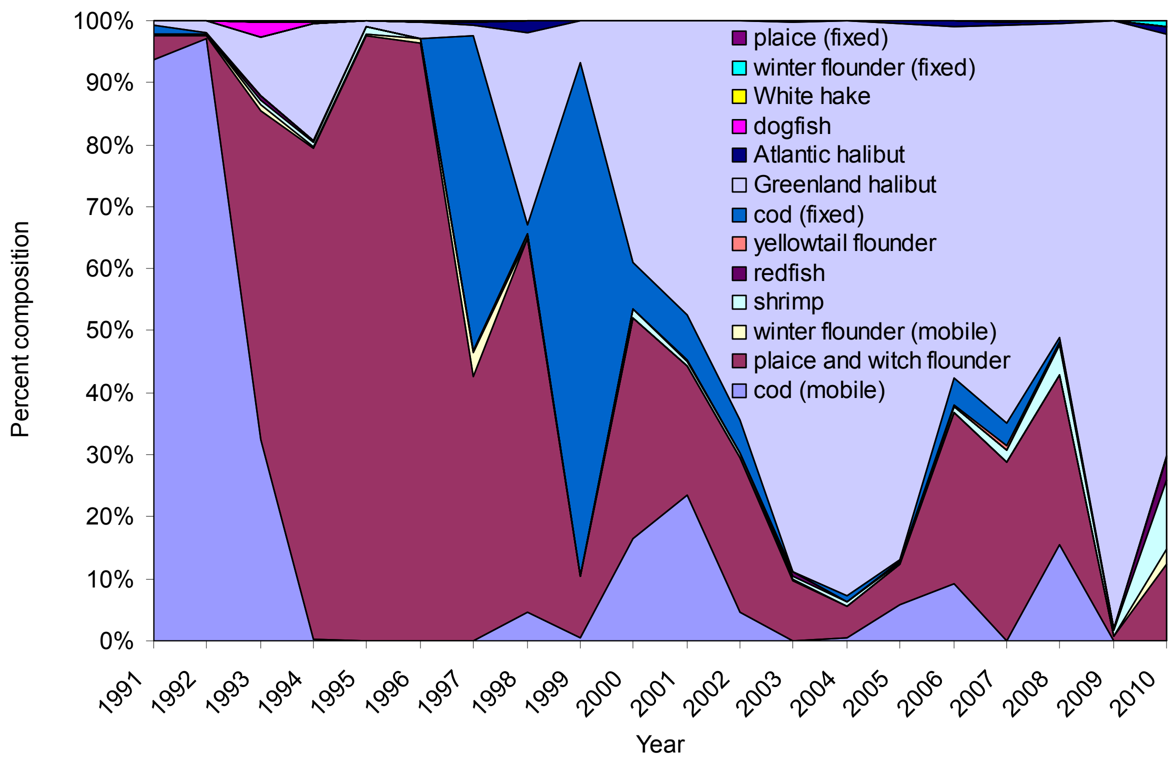

Figure 21. Relative contribution of different sGSL fisheries to thorny skate discards, 1991-2010.

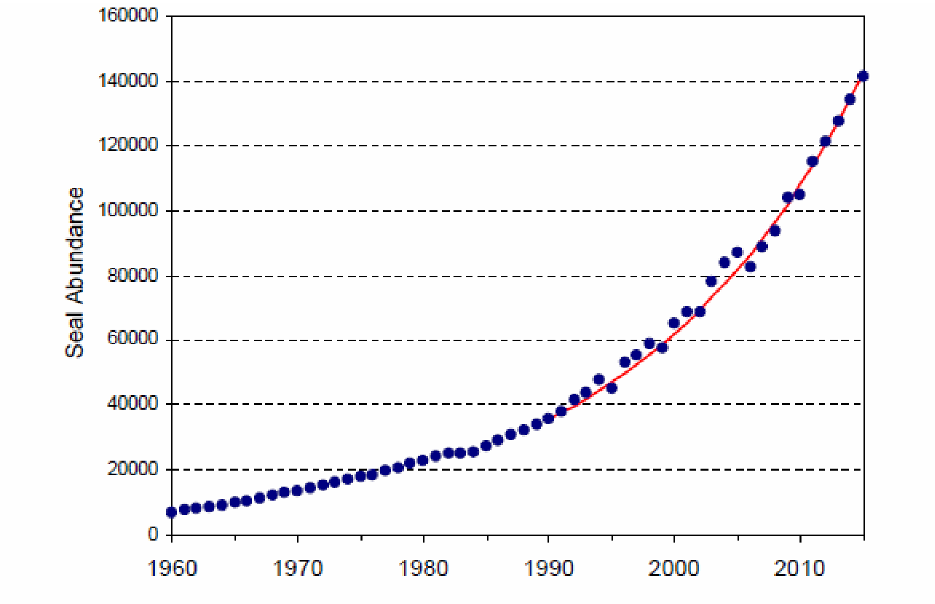

Figure. 22. Estimated abundance of grey seals occurring at some time of the year in the southern Gulf as well as the neighbouring Sydney Bight area during winter (December-April). From Swain et al. 2011.

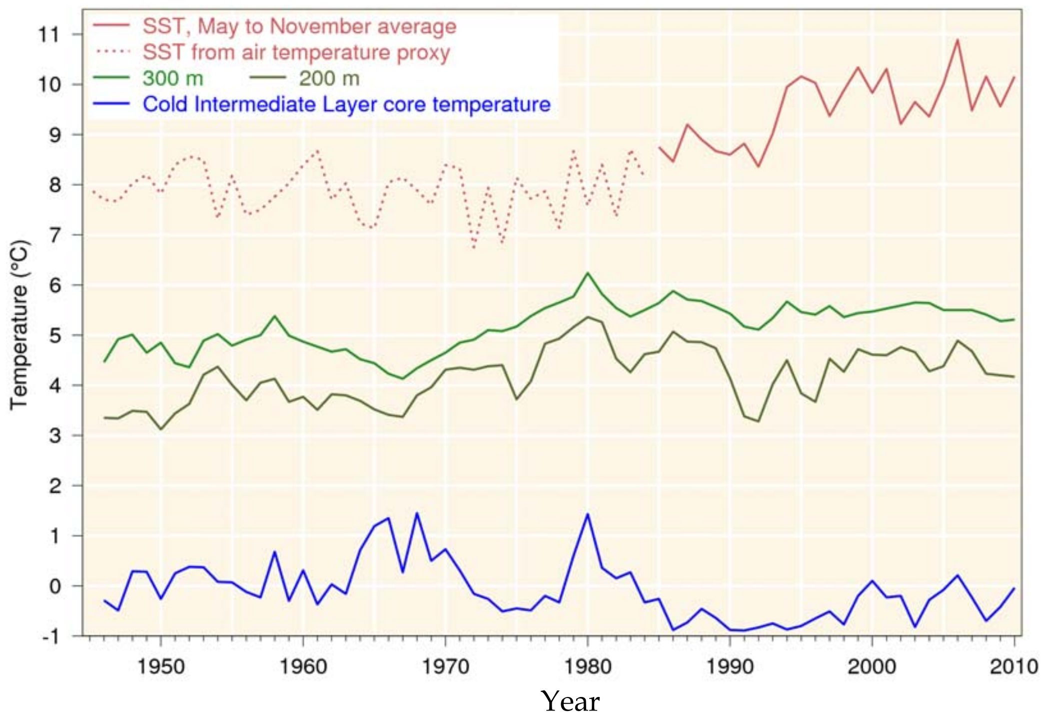

Figure. 23. Water temperatures in the Gulf of St. Lawrence. May-November sea surface temperature (SST) averaged over the Gulf (1985–2010, red line), completed by a proxy based on April-November air temperature (1945–1984, red dashed line). Layer-averaged temperature for the Gulf of St. Lawrence at 200 and 300m (green lines). Cold intermediate layer minimum temperature index in the Gulf of St. Lawrence (blue line). SST from Galbraith et al. (2012), and other time series from Galbraith et al. (2011). Figure courtesy of P. Galbraith (DFO, Quebec Region).

Appendix I: Skate maturity stages

Code	Stage	Male	Female
1	Immature	Claspers are undeveloped, shorter than extreme tips of posterior pelvic lobes. Testes small, thread shaped.	Ovaries small, with their surface undeformed and smooth. No eggs visible on the dorsal or ventral surface. Ovary thinner than stage 2.
2	Maturing 1	Claspers are more or less extended, longer than tips of posterior pelvic lobes. Their tips (glans) are more or less structured, but their skeleton is still flexible, soft. Testes are enlarged, sperm ducts beginning to meander.	Clear eggs up to 2 millimeters in diameter are visible in the top surface (dorsal) of the ovaries. Surface of ovaries smooth and undeformed. ***Caution: When observing from the ventral surface the ovary must be flipped over.***
3	Maturing 2	No stage.	Eggs grow in size (2-5 mm) and are cream coloured. Texture and content resemble small chicken yolks except for colour. Dorsal surface of ovary irregular. Ventral surface of ovary may still be smooth in early stage but slicing ovary with knife immediately reveals eggs.
4	Mature	Claspers full length, glans structure fully formed, skeleton hardened so that claspers are stiff. Testes greatly enlarged, sperm ducts meandering and tightly filled with flowing sperm.	Eggs grow in size (5-20 mm) and turn chicken yolk creamy yellow in colour and texture. Ovaries swollen and deformed on all surfaces. Blood vessels appear on yolk surface in later stage. Yolk may be seen in the fallopian tubes.
5	Spawning	Glans often dilated, its structures reddish and swollen. Sperm present in clasper groove or glans and flows on pressure from the cloaca.	Yolk in fallopian tubes beginning to be enveloped by purse. This begins at the rear and continues until entire yolk is surrounded by purse. The number of purses should be noted in comments. When complete the purse is discharged.