ICES Journal of Marine Science, 57: 24–30. 2000
doi:10.1006/jmsc.2000.0667, available online at http://www.idealibrary.com on IDEAL®

Changes in inferred spawning areas of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) due to changing environmental conditions

Y. Sakurai, H. Kiyofuji, S. Saitoh, T. Goto, and Y. Hiyama

Sakurai, Y., Kiyofuji, H., Saitoh, S., Goto, T., and Hiyama, Y. 2000. Changes in inferred spawning areas of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) due to changing environmental conditions. – ICES Journal of Marine Science, 57: 24–30.

Annual catches of *Todarodes pacificus* in Japan have gradually increased since the late 1980s. Paralarval abundances have also been higher since the late 1980s compared to the late 1970s and mid-1980s. Here is proposed a possible scenario for the recent stock increase based on changing environmental conditions. Based on trends in annual variations in stock and in larval abundances, catches are reviewed and potential spawning areas inferred, assuming that egg masses and hatchlings occur over the continental shelf at temperatures between 15 and 23°C. Changes are then inferred in the spawning areas during 1984–1995, based on GIS data. Since the late 1980s, the autumn and winter spawning areas in the Tsushima Strait and near the Goto Islands appear to have overlapped, and winter spawning sites seem to have expanded over the continental shelf and slope in the East China Sea.

Key words: GIS, paralarvae, regime shift, spawning areas, fluctuations, *Todarodes pacificus*.

Received 29 January 1999; accepted 11 January 2000

Y. Sakurai, H. Kiyofuji, and S. Saitoh: Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido 041-8611, Japan. T. Goto, and Y. Hiyama: Japan Sea National Fisheries Research Institute, Niigata 951-8121, Japan. Correspondence to Y. Sakurai: tel: +81 138 40 8863; fax: +81 138 40 8860; e-mail: sakurai@pop.fish.hokudai.ac.jp

Introduction

Most commercially exploited squid live for less than two years (Boyle, 1987). In such short-lived species, recruitment success probably depends on the physical and biological environments at the spawning and nursery grounds. Since the "failures" of the *Todarodes pacificus* and *Illex illecebrosus* fisheries in the 1980s, the role of environmental change on squid stocks has become an increasingly important topic of research (Lipinski *et al*., 1998; Roberts, 1998).

Todarodes pacificus is a commercially important squid in Japan. Annual catches have fluctuated widely since the 1900s and increased markedly during 1986–96 (Fig. 1). Three populations with different peak spawning seasons (summer, autumn and winter) migrate seasonally between the Sea of Japan and the Pacific Ocean, with most spawning occurring near Kyushu Island (Okutani and Watanabe, 1983; Murata, 1989, 1990). Annual variations in stock density are usually estimated

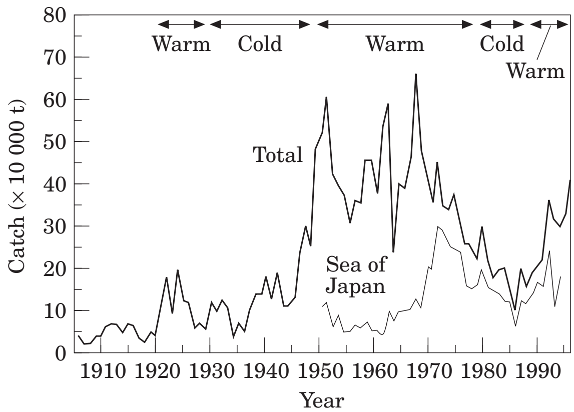

Figure 1. Annual fluctuations in Japanese *Todarodes pacificus* catches in the Sea of Japan and the total from 1900 onwards (modified from Murata, 1989; catches before 1951 include other squid species). Horizontal lines indicate interdecadal regime shifts in water temperature in the Western North Pacific (Minobe, 1997).

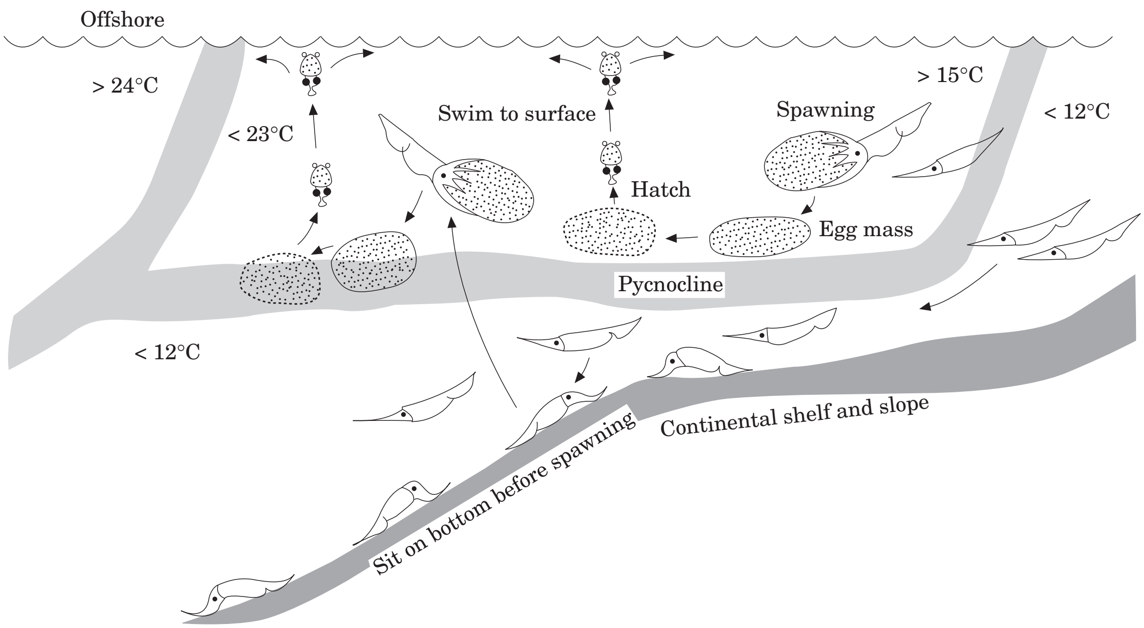

Figure 2. Schematic view of reproduction processes of *Todarodes pacificus* (working hypothesis based on results of experimental studies).

using average catch weight-per-fishing boat-per-day (c.p.u.e.) throughout the fishing season (Murata, 1989, 1990), because c.p.u.e. appears to be a better stock index of the autumn and winter spawning groups than annual catches (Okutani and Watanabe, 1983; Murata, 1989, 1990). Paralarval abundance is also used to assess the stock–recruitment relationship (e.g. Murata, 1989, 1990).

Episodic "regime shifts" involving entire biological community structures occur worldwide (Lluch-Belda *et al.*, 1992). In the western North Pacific environmental conditions have shifted from a warm regime, which began in the late 1940s, to a cool regime in the late 1970s, and then back to a warm regime in the late 1980s (see Minobe, 1997). These regime shifts appear to coincide with variation in *T. pacificus* catches: catches decreased particularly during the early 1980s and increased during the late 1980s catch (Fig. 1). Paralarval abundance of the autumn spawning group has also been higher since the late 1980s compared to the period of the late 1970s to the mid-1980s. These stock fluctuations might be related to the effects of regime shifts on spawning and paralarval survival.

We review recent trends in annual variation in *T. pacificus* stock size and paralarval density, and propose a possible scenario for stock fluctuations based on two assumptions: (i) stock size increases with a shift to a warm regime; and (ii) environmental conditions during warm regimes are favourable for reproduction, paralarval survival, and therefore recruitment. We then estimate the relationship between recent seasonal and annual changes in the inferred extent of the spawning grounds based on water temperatures around Japan.

Materials and methods

To analyze the stock–recruitment relationship, paralarval density index (PDI) values in the northern part of the East China Sea and the southwestern Sea of Japan during autumn, and annual c.p.u.e. values of the autumn-spawning group in the Sea of Japan were examined. PDI was calculated as the number of paralarvae per 1000 m^3 of water filtered in oblique tows of an 80 cm diameter plankton net with 0.345 mm (1975–1984), 0.508 mm (1985–1996) mesh from 75 m depth to the surface. The parameter c.p.u.e. is the mean catch (t) per fishing day by 70 to 100-ton vessels using automatic jigging machines in offshore waters of the Sea of Japan each August.

Potential spawning areas were estimated using information collected from laboratory and field studies. *T. pacificus* produce gelatinous, nearly neutrally buoyant egg masses (Bower and Sakurai, 1996). The temperature range for normal embryonic development is 15–23°C (Sakurai *et al.*, 1996), while most hatchings collected off southern Japan occur at sea surface temperatures of 17–23°C (Bower, 1997). The temperatures at 50 m depth were used to estimate the range of spawning grounds, since most paralarvae occur at 25–50 m depth (Watanabe, 1965). Spawning is assumed to occur above the continental shelf and slope around Japan (Fig. 2),

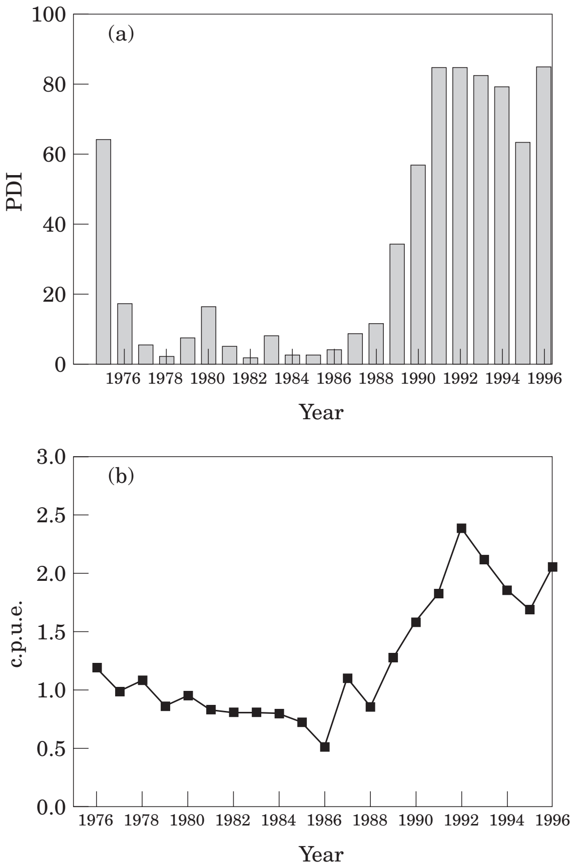

Figure 3. Time series of abundance indices of *Todarodes pacificus*. (a) Paralarval density indices (PDI: number per 1000 m^3 of water) during autumn in the northern East China Sea and the southwestern Sea of Japan, 1975–1996; (b) annual c.p.u.e. (t per fishing day, August) for the autumn-spawning group in offshore waters of the Sea of Japan, 1976–1996.

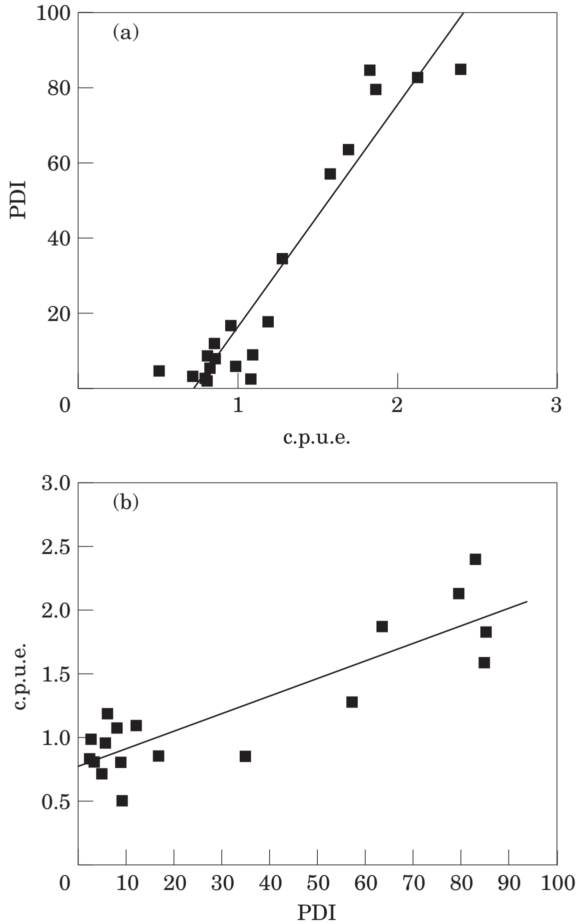

Figure 4. Relationship between abundance indices of *Todarodes pacificus*, 1975–1996 (cf. Fig. 3). (a) PDI and c.p.u.e. in the same year ($Y=58.9X-42.5$, $R^2=0.91$, $p<0.01$); (b) c.p.u.e. and PDI in the year before ($Y=0.01X+0.78$, $R^2=0.77$, $p<0.01$).

because captive females regularly sit on the tank bottom just before spawning (Bower and Sakurai, 1996). Also, bottom trawls often collect exhausted, spent (post-spawning) females on the shelf and slope at 100–500 m depth (Hamabe and Shimizu, 1966). To estimate historical, inferred spawning areas, mean monthly temperature data at 50 m depth during 1900–1972 (JODC, 1978) over the continental shelf around Japan were examined.

Monthly and annual estimates of inferred spawning areas between 21–53°N and 121–153°E during 1984–1995 were derived using three data sets: monthly GMCSST (global multi-channel sea surface temperature), Levitus, and hydrographic and topographic data. NOAA/NESDIS (National Environmental Satellite Data and Information Service) and NODC (National Oceanographic Data Center) provided the GMCSST and Levitus data sets. We developed a linear equation to relate temperatures at 0 m and 50 m depth and used this relation to estimate the 50-m depth temperature for each month during 1984–1995 based on GMCSST data. The surface area where the 50-m depth temperature of 15–23°C occurred above bottom depths of 100–500 m represents the inferred spawning area.

Results and discussion

Annual PDI values were relatively high in 1975, low during 1976–1988, and increased remarkably after 1989, a pattern that largely corresponds to changes in annual c.p.u.e. values (Fig. 3). During 1973–1984, a positive relationship existed between both adult catch and PDI of their offspring, and between PDI and adult catch of the same generation for the autumn-spawning group (Murata, 1989). During 1975–1996, PDI was strongly correlated ($R^2=0.91$, $p<0.01$) to c.p.u.e. in the summer of the same year, while a less strong, but still significant positive relationship ($R^2=0.77$, $p<0.01$) also existed between PDI and c.p.u.e. in the next summer (Fig. 4).

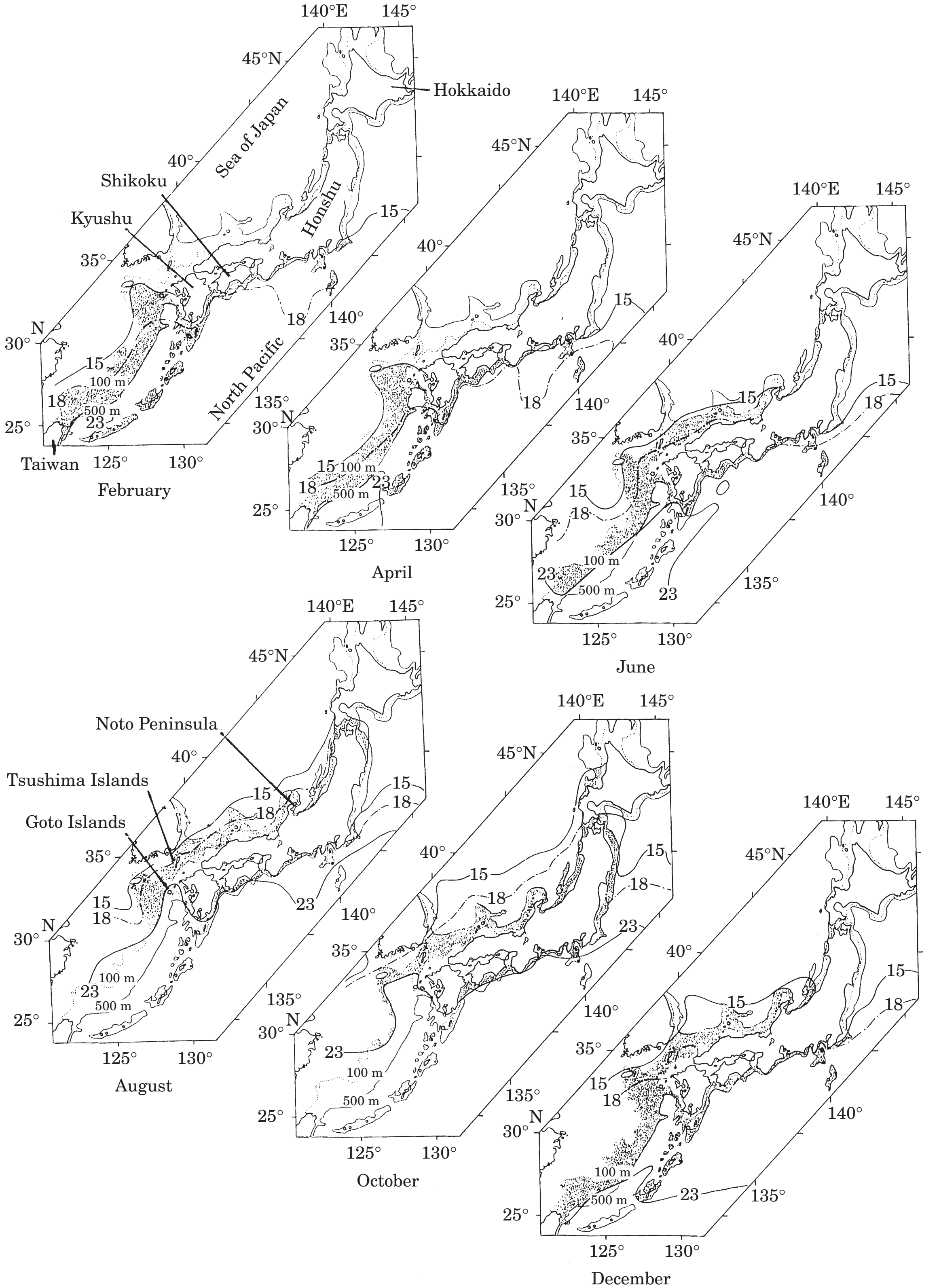

Figure 5. Inferred monthly spawning areas of *Todarodes pacificus* around Japan based on mean temperature for embryonic development (15–23°C) over the continental shelf and slope isobaths of 100–500 m.

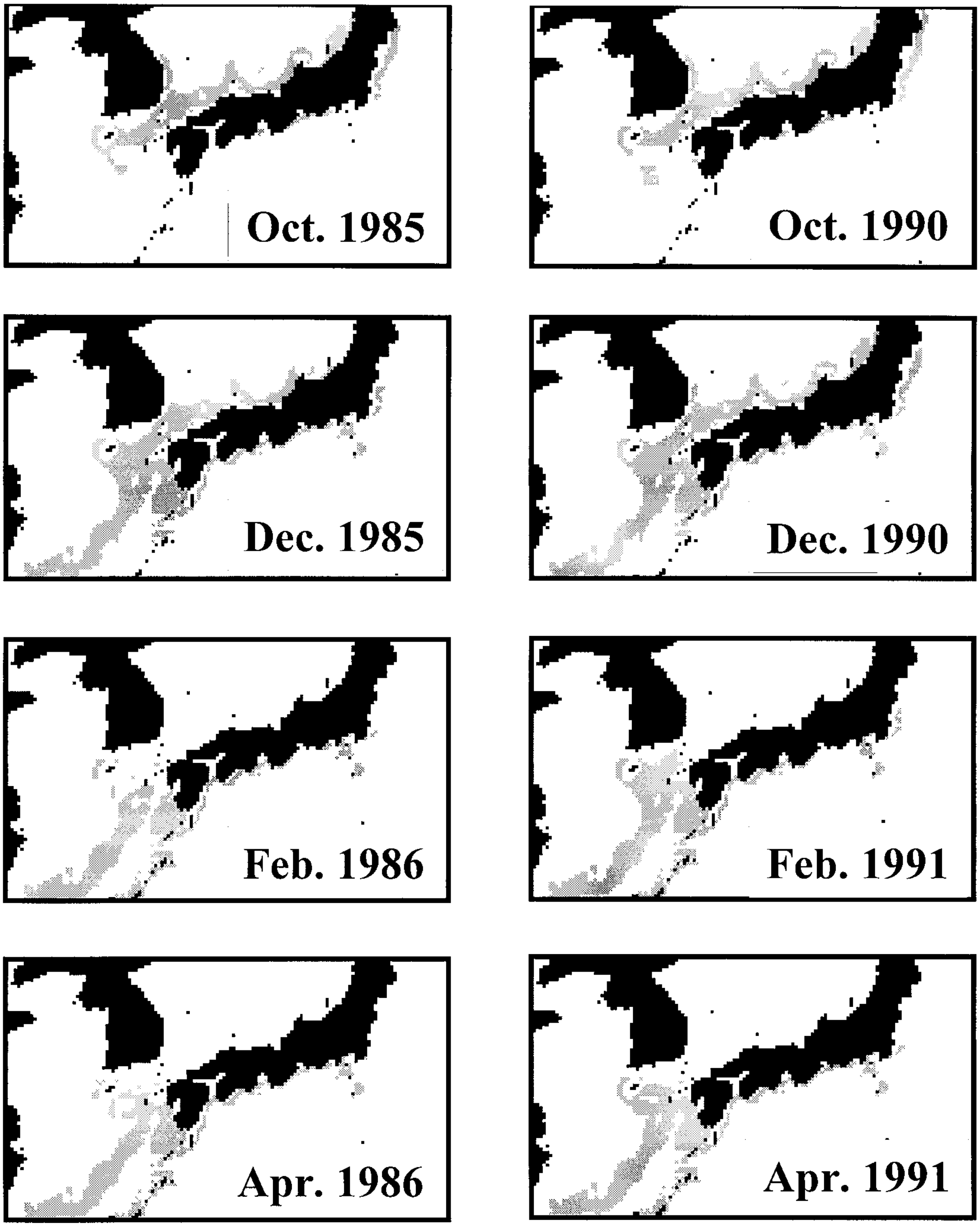

Figure 6. Comparison of seasonal shifts in inferred spawning areas (white) between October to April in 1985/1986 (cold year) and 1990/1991 (warm year), based on GIS data. Black and white areas represent land and unsuitable depths/temperatures, respectively.

These results suggest that catch increases since the late 1980s could reflect a possible relationship between stock and PDI and between PDI and recruitment. The winter-spawning group (spawning mainly occurs in the East China Sea) had the largest stock size of the three groups during the late 1960s, but the autumn-spawning group (mainly offshore in the south-western Sea of Japan) was the largest in the 1970–1980s (Murata, 1989). The results here indicate that the inferred spawning areas of the autumn and winter-spawning groups have both expanded and now overlap spatially in the Tsushima Strait. This suggests that the recent stock increase may have occurred in both the autumn and winter spawning groups.

Table 1. Summary of interannual variability in extension of inferred spawning areas in February, 1984–1994.

Year	East China Sea	Tsushima Strait		
		South	Central	North
1984	++	−	−	−
1985	++	++	−	−
1986	++	++	−	−
1987	++	++	+	−
1988	++	+	−	−
1989	++	++	++	++
1990	++	++	++	−
1991	++	++	++	−
1992	++	−	−	−
1993	++	++	−	−
1994	++	++	++	++

++: area largely favourable for spawning; +: partly favourable; −: not favourable.

The main inferred spawning areas for the winter-spawning group occurred widely along the continental shelf and slope of the East China Sea from Kyushu to Taiwan, and small spawning areas occurred in the western and the south-western coastal waters of Kyushu and Pacific coastal waters off Shikoku (Fig. 5). During spring to summer, the spawning area gradually shifted northwards along the continental shelves of the Sea of Japan and Pacific Ocean. In autumn, the inferred spawning areas occurred around the Tsushima Strait and Noto Peninsula, while limited spawning might also have occurred along the coast of northern Japan. These results support the conclusions of Murata (1989, 1990), based on changes in paralarval distribution, that the main spawning grounds during autumn were in the Tsushima Strait to the south-western Sea of Japan, and during winter, in the East China Sea. Spawning areas of the three groups may seasonally shift and do exhibit overlap. However, potential spawning grounds along central and northern Japan are restricted due to the narrow continental shelf zone and the low temperatures during winter to spring.

GIS data were used to examine the relationship between the recent seasonal and annual changes of the inferred spawning areas during 1984 to 1995 and the shift from a cold regime to a warm regime that occurred in the late 1980s. Kiyofuji *et al.* (1998) have already concluded that the inferred spawning grounds occurred year-round in the Tsushima Strait and near the Goto Islands in 1989–1991, which was the beginning of the warm regime when autumn paralarval abundance and annual catch increased. However, the inferred spawning areas did not vary geographically between 1985/1986 and 1990/1991 from October to December (Fig. 6). In February 1991, inferred spawning areas ranged from the Tsushima Strait to the East China Sea. Although the pattern was broadly similar in 1986, they did not extend into the Tsushima Strait. Table 1 summarizes the information on interannual variability in inferred spawning areas in February (the peak spawning month of the winter-spawning group; Murata, 1989) during 1984–1994, and more detailed information for selected years is given in Fig. 7. In 1989, 1990, 1991, and 1994, suitable areas for spawning were spread widely from the Tsushima Strait to the East China Sea. In contrast,

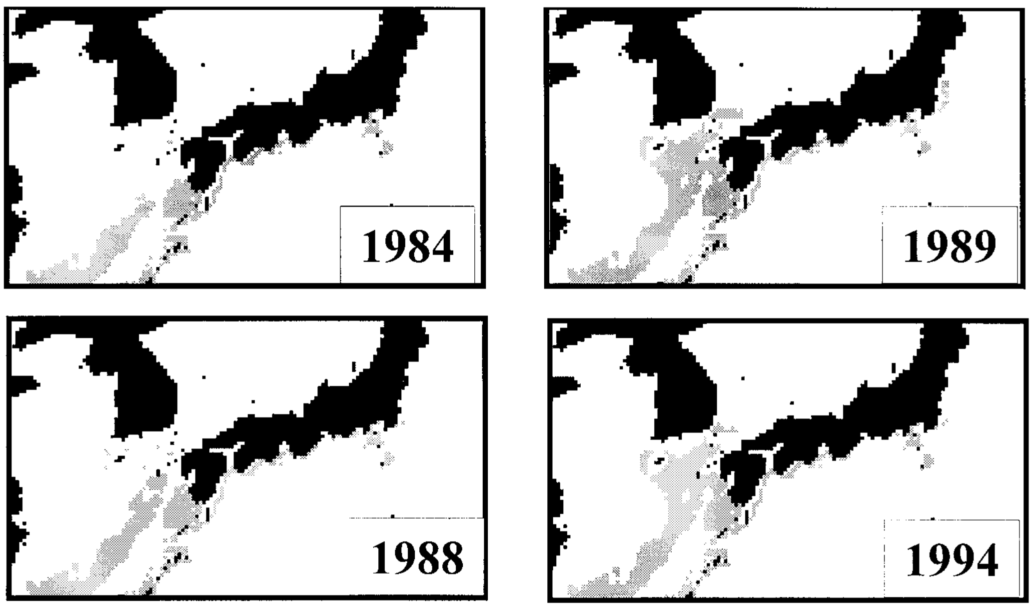

Figure 7. Interannual variability of inferred spawning areas in February in 1984/1988 (cold years), and in 1989/1994 (warm years), based on GIS data (see also Fig. 4).

conditions in Tsushima Strait were particularly unfavourable in 1984, 1988, and in 1992, although spawning may have occurred above the continental shelf in the East China Sea and southwest of Kyushu.

The results suggest that winter-spawning areas in the East China Sea shrink when adult stocks decrease during a cool regime, and that autumn and winter-spawning areas extend and overlap in the Sea of Japan and East China Sea when adult stocks increase during a warm regime. Although a series of warm winters may promote stock increase, the high interannual variability may be responsible for large fluctuations in catches. For instance, in the middle of a relatively warm period, the inferred spawning areas in February 1992 was strongly reduced.

GIS is increasingly being used for oceanographic and fisheries studies (Simpson, 1994; Kiyofuji *et al.*, 1998; Waluda and Pierce, 1998). This study shows that it has potential to elucidate historic stock fluctuations in *T. pacificus* in relation to climatic regime shifts by examining temporal and spatial distribution of the optimum temperature areas for reproduction.

Acknowledgements

We thank Y. Isoda, Y. Nakamura, K. Mori, and U. Piatkowski at the Institute for their valuable comments. We also thank John R. Bower, Richard E. Young and an anonymous reviewer for their reviews of the manuscript. The study was supported in part by Grant-in-Aid for Scientific Research from the Ministry of Education, Science, Sports, and Culture of Japan (09460080).

References

Bower, J. R. 1997. A biological study of egg masses and paralarvae of the squid *Todarodes pacificus*. Doctoral Thesis, Hokkaido University. 171 pp.

Bower, J. R., and Sakurai, Y. 1996. Laboratory observations on *Todarodes pacificus* (Cephalopoda: Ommastrephidae) egg masses. American Malacological Bulletin, 13: 65–71.

Boyle, P. R. (ed.) 1987. Cephalopod life cycles, Vol. II: Comparative reviews. Academic Press, London. 441 pp.

Hamabe, M., and Shimizu, T. 1966. Ecological studies on the common squid, *Todarodes pacificus* Steenstrup, in the south-eastern waters of the Japan Sea. Bulletin of the Japan Sea Regional Fisheries Research Laboratories, 16: 13–55 (in Japanese with English abstract).

JODC (Japan Oceanographic Data Center) 1978. Marine Environmental Atlas, Northwestern Pacific Ocean (Seasonal and Monthly). Japan Hydrography Association, Tokyo. 147 pp. (in Japanese with English abstract).

Kiyofuji, H., Saitoh, S., and Sakurai, Y. 1998. A visualization of the variability of spawning ground distribution of Japanese common squid (*Todarodes pacificus*) using Marine-GIS and Satellite data sets. Proceedings of International Symposium Real-Time Imaging and Dynamics Analysis, International Society of Photogrametry and Remote Sensing Commission, V: 882–887.

Lipinski, M. R., Butterworth, D. S., Augustyn, C. J., Brodziak, J. K. T., Christy, G., des Clers, S., Jackson, G. D., O'Dor, R. K., Pauly, D., Purchase, L. V., Roberts, M. J., Roel, B. A., Sakurai, Y., and Sauer, W. H. H. 1998. Cephalopod fisheries: a future global upside to past overexploitation of living marine resources? Results of an International Workshop, 31 August–2 September 1997, Cape Town, South Africa. South African Journal of Marine Science, 20: 463–469.

Lluch-Belda, D., Schwartzlose, R. A., Serra, R., Parrish, R., Kawasaki, T., Hedgecock, D., and Crowford, R. J. M. 1992. Sardine and anchovy regime fluctuations of abundance in four regions of the world's oceans: a workshop report. Fisheries Oceanography, 1: 339–347.

Minobe, S. 1997. A 50–70 year oscillation over the north Pacific and north America. Geophysical Research Letters, 24: 683–686.

Murata, M. 1989. Population assessment, management and fishery forecasting for the Japanese common squid, *Todarodes pacificus*. *In* Marine Invertebrate Fisheries: their Assessment and Management, pp. 613–636. Ed. by J. R. Caddy. John Wiley and Sons, New York.

Murata, M. 1990. Ocean resources of squids. Marine Behavior and Physiology, 18: 19–71.

Okutani, T., and Watanabe, T. 1983. Stock assessment by larval surveys of the winter populaton of *Todarodes pacificus* Steenstrup (Cephalopoda: Ommastrephidae), with a review of early works. Biological Oceanography, 2: 401–431.

Roberts, M. J. 1998. The influence of the environment of chokka squid *Loligo vulgaris reynaudii* spawning aggregations: steps towards a quantified model. South African Journal of Marine Science, 20: 267–284.

Sakurai, Y., Bower, J. R., Nakamura, Y., Yamamoto, S., and Watanabe, K. 1996. Affect of temperature on development and survival of *Todarodes pacificus* embryos and paralarvae. American Malacological Bulletin, 13: 89–95.

Simpson, J. J. 1994. Remote sensing in fisheries: a tool for better management in the utilization of a renewable resources. Canadian Journal of Fisheries and Aquatic Sciences, 51: 747–771.

Waluda, C. M., and Pierce, G. J. 1998. Temporal and spatial patterns in the distribution of squid *Loligo* spp. in United Kingdom waters. South African Journal of Marine Science, 20: 323–336.

Watanabe, T. 1965. Ecological distribution of rhynchoteution larva of common squid, *Todarodes pacificus* Steenstrup, in the southeastern waters off Japan during the winters, 1959–1962. Bulletin of Tokai Regional Fisheries Research Laboratory, 43: 1–12 (in Japanese with English abstract).