



Larval recruitment and fisheries of the spiny lobster *Panulirus japonicus* coupling with the Kuroshio subgyre circulation in the western North Pacific: A review

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Abstract

Panulirus japonicus is an important target for fisheries in Japan. Characteristics of long distance larval transport and recruitment of *P. japonicus* have been revealed based on drifter studies and larval sampling. Larval recruitment of the lobster is completed within the Kuroshio Subgyre circulation, *i.e.*, early stage phyllosomas that are released in Japanese coastal waters in summer (July-September) are transported into the Kuroshio region; larvae are then transported to the Kuroshio Counter-Current region south of the Kuroshio; these larvae are then transported into the waters east of the Ryukyu Archipelago where subfinal/final-stage phyllosomas and pueruli enter the Kuroshio again and are transported to different locations of Japanese coastal waters through the Kuroshio in the summer of the following year. Using mtDNA sequences for the COI region of *P. japonicus* juveniles and adults, no significant population subdivision was detected among distant locations. There was no characteristic geographical distribution pattern for haplotypes, supporting the hypothesis that these benthic individuals are sustained by a common pool of phyllosomas through long distance larval transport by phyllosomas within the Kuroshio Subgyre circulation. This scenario is also supported by the examination of long-term variation in *P. japonicus* catches as follows. Two clusters (A, B) of regions located east (A) and west (B) of the cape Shionomisaki at the southern tip of the Kii Peninsula were identified. There was a significant positive relationship between the Kuroshio index and the catch index two years later for cluster A. This relationship suggests that annual variation in *P. japonicus* catch may be determined by the variation in puerulus recruitment through the Kuroshio. Relationships between these two clusters varied depending on three periods, which corresponded to the three climate regimes (*i.e.*, years before 1976, from 1977 to 1988, and after 1989). Significant negative relationships were detected between the catch index of these two clusters from 1975 to 2001.

Keywords: Spiny lobster, long distance larval transport, recruitment, Kuroshio, genetic population structure

Introduction

In Japanese waters, nine *Panulirus* species have been reported (Sekiguchi, 2008): *P. brunneiflagellum* Sekiguchi and George, 2005; *P. femrostriga* (von Martens, 1872); *P. homarus homarus* (Linnaeus, 1758); *P. japonicus* (von Siebold, 1824); *P. longipes bispinosus* (Borradaile, 1899); *P. ornatus*, (Fabricius, 1798); *P. penicillatus* (Olivier, 1791); *P. stimpsoni* (Holthuis, 1963) and *P. versicolor* (Latreille, 1804). Of the nine species of *Panulirus* in Japanese waters, *P. japonicus* is found commonly in waters under the influence of the Kuroshio and its branches. The

other species (except *P. brunneiflagellum* confined to Ogasawara waters far east of the Ryukyu Archipelago, see Fig. 1. for location) are found mainly in southern Japan, particularly in the Ryukyu where their annual catch is very low to amount to nearly tonnes (Sekiguchi, 1988, 1989). Total annual catch of spiny lobsters in Japan is approximately 1,000 t, and is dominated by *P. japonicus*. The other palinurid lobsters (the genera of *Justitia*, *Linuparus*, *Palinustus* and *Puerulus*), the *Palinurellus* of the Synaxidae as well, have been known in Japan (Sekiguchi and Inoue, 2002), although these are

targets for recreational fishing in local areas. This is also true of large-sized scyllarid lobsters such as the genera of *Ibacus*, *Parribacus* and *Scyllarides* in Japan.

The early life history of *P. japonicus* have already been reviewed by Sekiguchi (1997) and Sekiguchi and Inoue (2002), this paper reviews the early life history and larval recruitment of the spiny lobster *P. japonicus* using the data accumulated since 2001,

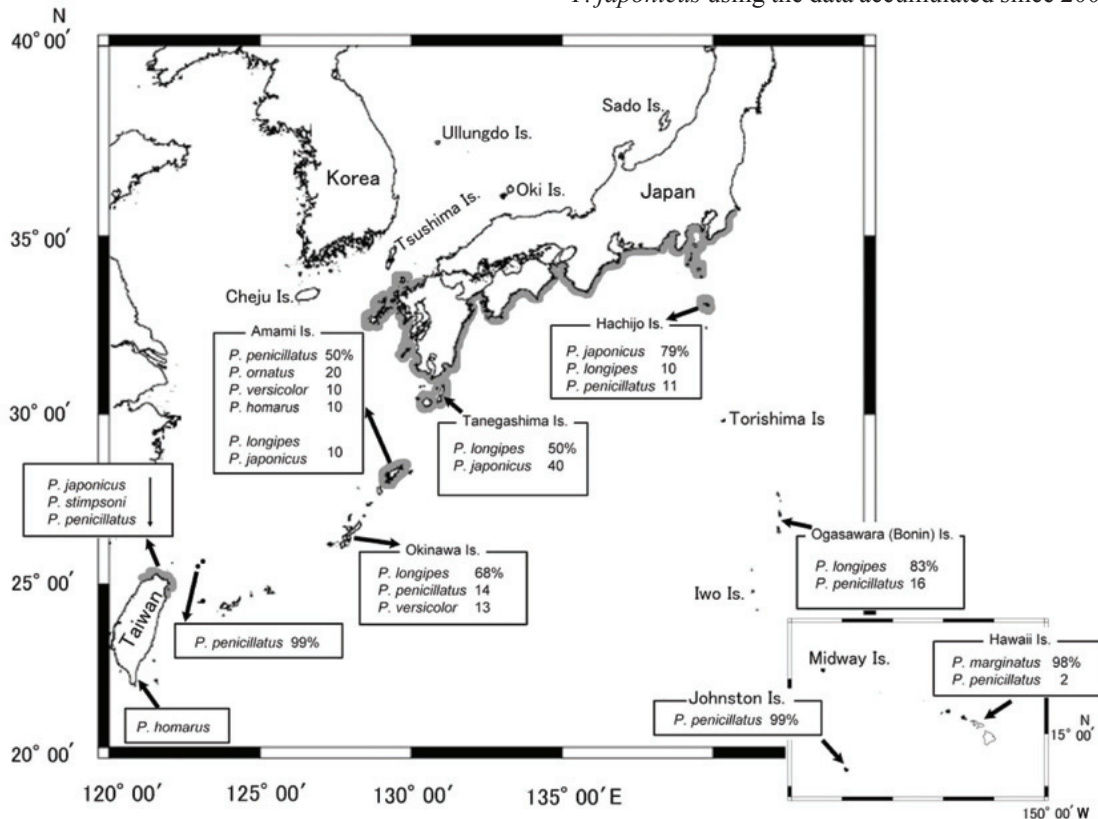


Fig. 1. Relative abundance of *Panulirus* species in Japan and its neighbouring waters (modified from Sekiguchi, 1988). Shading areas indicate the habitats of *P. japonicus*. *P. longipes* from Ogasawara Islands in the figure have been identified with *P. brunneiflagellum* and *P. longipes bispinosus* (Sekiguchi and George, 2005)

Panulirus japonicus is one of most the highly valued crustaceans in Japan as compared to the other sea foods. As a result, there is much interest in the biology and fisheries management of this species. Japanese scientists have worked to unveil the mysteries of larval dispersal of *P. japonicus* and several important aspects of its larval biology, ecology, and population dynamics have emerged in the last two decades (Sekiguchi and Inoue, 2002). Sekiguchi has advanced a hypothesis describing the path of long distance larval transport that has been supported by direct evidence in field surveys (Yoshimura *et al.*, 1999; Inoue and Sekiguchi, 2001, 2009; Inoue *et al.*, 2007).

adding to previous knowledge and focusing on the long distance larval transport/dispersal and recruitment completed within the Kuroshio Subgyre circulation (the Kuroshio Current coupling with the Counter Current south of the Kuroshio) in the western North Pacific. This paper deals with geographical distribution of the species as related to the coral reef distribution, current systems around Japanese waters, identification of phyllosoma and puerulus, long distance larval transport of the species within the Kuroshio Subgyre circulation, genetic population structure of the species and long-term variation in catches of the species regulated by puerulus supply variation coupled with the Kuroshio Current.

Geographical distribution of *Panulirus* species as related to the coral reef distribution in the western North Pacific

P. japonicus is the northernmost and temperate species of the genus *Panulirus* found in tropical waters of the world, and the geographical distribution of *P. japonicus* is confined to coastal waters inshore/north of the Kuroshio current (Fig. 1). According to Sekiguchi (1988; 1989; 1995), it is probable that habitats of either coral or rocky reefs determine the presence of *P. longipes* subspecies and *P. japonicus* respectively.

Coral reefs are common in the Ryukyu Archipelago, while in Taiwan they are confined to around its southern tip. The northern boundary of coral reefs in the western north Pacific is located at

the Tokara strait between Amami-Oshima and Yakushima Islands, and the eastern boundary is between Torishima and Ogasawara Islands (Takahashi, 1988). *P. japonicus* has been found in waters without coral reefs but with rocky reefs, and the southern boundary of the distribution of *P. japonicus* coincides with the northern boundary of the coral reef distribution in the western north Pacific and also with the northern boundary of the Kuroshio (Sekiguchi, 1988; 1989; Fig. 1 and 2). According to George (1967; 1974), the two subspecies of *P. longipes* are typical inhabitants of coral reef waters, though they prefer to be in the waters outside of coral areas. This is also true of *P. l. bispinosus* in the Ryukyu. On the other hand, *P. japonicus* typically inhabits rocky reefs open to the ocean (George, 1974; Sekiguchi, 1989).

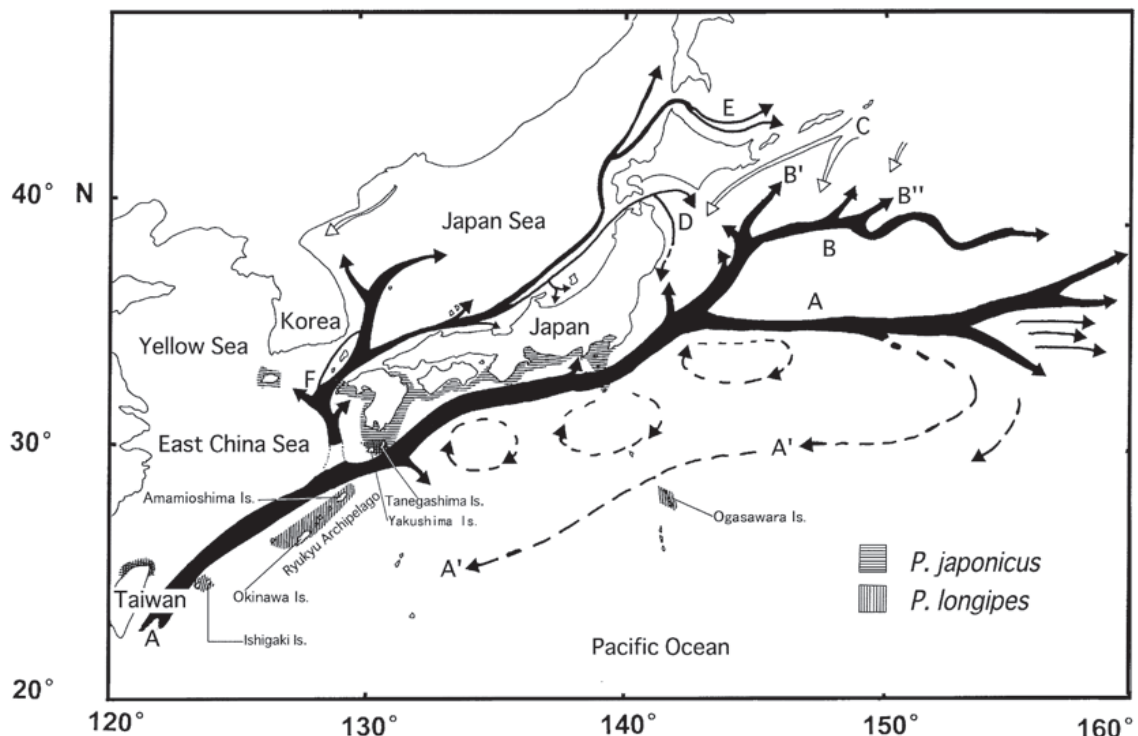


Fig. 2. Current systems in Japan and its neighbouring waters, with notes on geographical distributions of *Panulirus japonicus* and *P. longipes bispinosus* (modified from Sekiguchi and Inoue, 2002); shaded areas indicate the habitats of *P. japonicus*. A, A', warm Kuroshio Current and Kuroshio Counter Current, respectively; B, B', B'', branches of the Kuroshio; C, cool Oyashio Current; D, warm Tsugaru Current; E, warm Soya Current; F, warm Tsushima Current

Current systems around Japanese waters within the Kuroshio Subgyre circulation in the western North Pacific

Current systems in Japan and its neighbouring waters are illustrated in Fig. 2. The Kuroshio located east of Taiwan enters the east China sea after passing through the strait between northern Taiwan and the southern parts of the Ryukyu. After flowing along the continental shelf edge of the east China sea and then separating off the Tsushima Current that flows in the water west of Kyusyu and passes through the Tsushima Strait between Japan and Korea to enter the Japan Sea, the Kuroshio passes through the Tokara strait between Amami-Oshima and Yakushima Islands and then flows along the Pacific coast of the southern and central parts of Japan.

Satellite-tracking drifters have been deployed in several regions in the North Pacific, e.g., near the coast of California and off the south-eastern coast of Kyusyu, Japan (McNally *et al.*, 1983; Michida and Ishii, 1993). With selected trajectories and

computed velocities, it is possible to describe some aspects of the structure of the North Pacific Subtropical Gyre and its variability. A complete description of these drifters is found in Kirwan *et al.* (1978). As indicated in Fig. 3, trajectories of a composite of 16 selected drifters launched from 1976 through 1980 provided a large-scale description of the near-surface circulation in the North Pacific. Trajectories of four drifters which were deployed across the Kuroshio main axis at about 30°N lat., 132°E long. during February 1977 traced the Kuroshio along the southeastern coast of Japan. At the time, the Kuroshio was in its well-known meandering configuration (Kawai, 1991, Fig. 4.) and the drifters reproduced this transient feature. Three drifters passed through Izu Islands over the Izu Ridge (located north to south along Hachijo Island, Fig. 1. for location) and entered the region of the Kuroshio extension of east Japan. One drifter meandered south along the western side of the Izu Ridge, turned east, and then proceeded into the western North Pacific well south of the other three

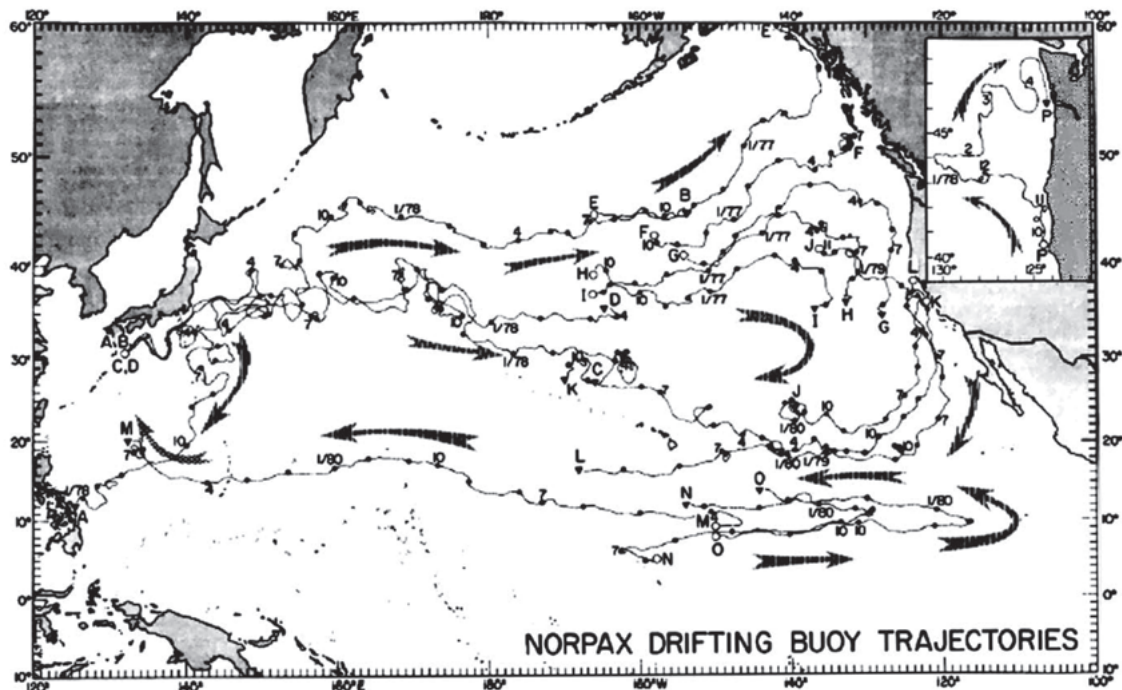


Fig. 3. Trajectories of 16 satellite-tracking buoys from 1976 through 1980 (from McNally *et al.*, 1983). Open circles: deploying locations, solid circles: the first day of each month, triangles: the last reported locations. The largest stippled arrows show the directions of the trajectories

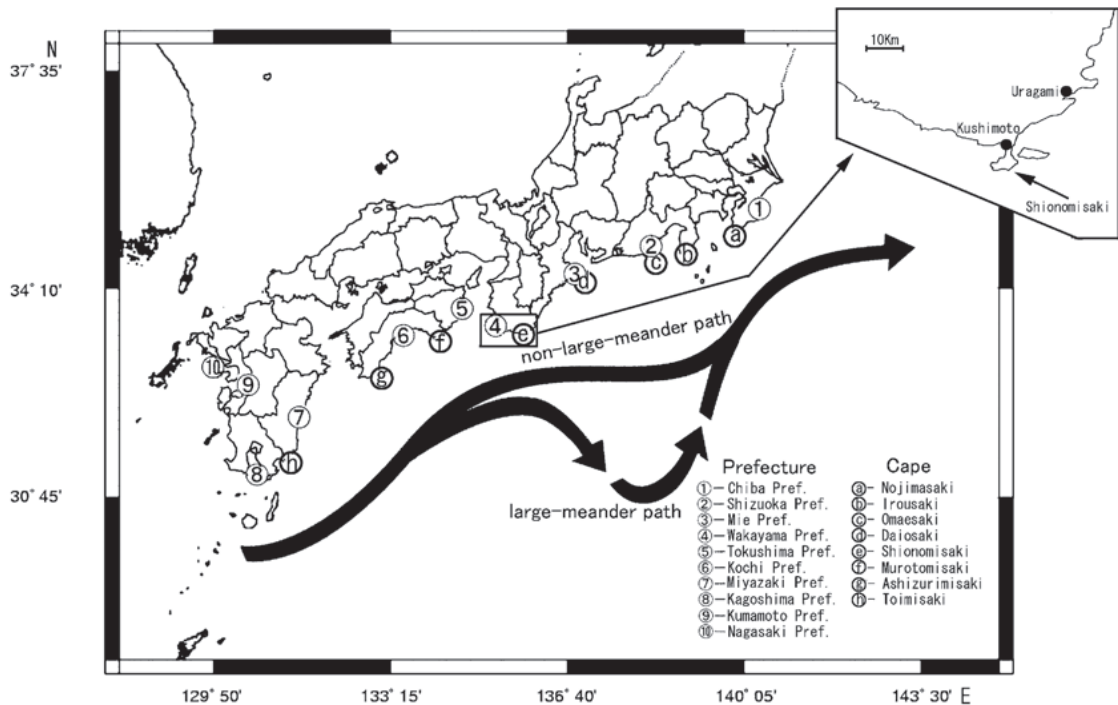


Fig. 4. Typical large meandering and non-large meandering paths of the main axis of the Kuroshio Current along the Pacific coast of Japanese islands (from Inoue and Sekiguchi, 2009). Numbers and letters: prefectures and capes, respectively

buoys. According to Ishii (1981), five of six drifters which were deployed across the Kuroshio main axis in March 1980 reproduced features of the above-mentioned trajectories. However, the remaining drifter passed over the Kuroshio main axis and entered the region of east Okinawa Islands where it turned in an anti-clockwise circulation for nearly six months. According to Andres *et al.* (2008) who examined a 12-year time series data of the East China Sea-Kuroshio transport, while the bulk of the Kuroshio entered the East China Sea through the strait between northern Taiwan and the southern parts of the Ryukyu, the effect of mesoscale eddies was transmitted to the East China Sea via the Kerama Gap southwest of Okinawa Islands. A branch (the Ryukyu Current) flows along the Pacific side of the Ryukyu, and there is evidence that the Ryukyu current is intensified as it flows northeastward along the Pacific side of the Ryukyu (Nagano *et al.*, 2007).

From Ishii (1981) and McNally *et al.* (1983) we can conclude that: (i) buoys did not reach Hawaiian

waters, at least not within 15 months after they were launched in the Kuroshio. (ii) a number of the buoys which were deployed in the Kuroshio entered the Kuroshio Counter Current south of the Kuroshio, turned southwest and took nearly one year to enter the water east of the Ryukyu. (iii) the buoys circulated around the Izu Ridge and in the waters of east Okinawa Islands for several months. Furthermore, as indicated in Fig. 5, the North Pacific Subtropical Gyre is composed of three subgyres (Hasunuma and Yoshida, 1978). From north to south, there are the Kuroshio-Counter Current Subgyre (hereafter the Kuroshio Subgyre), the Subtropical Current Subgyre, and the North Tropical Current. Thus, the Counter Current that is joined to the Kuroshio would consist mostly of the Kuroshio water, *i.e.*, forming the Kuroshio Subgyre circulation.

The Ryukyu Archipelago is located east of the Kuroshio, while Ogasawara Islands are south of the Kuroshio Counter Current. Based on the above-mentioned water circulation and/or subgyres, if the

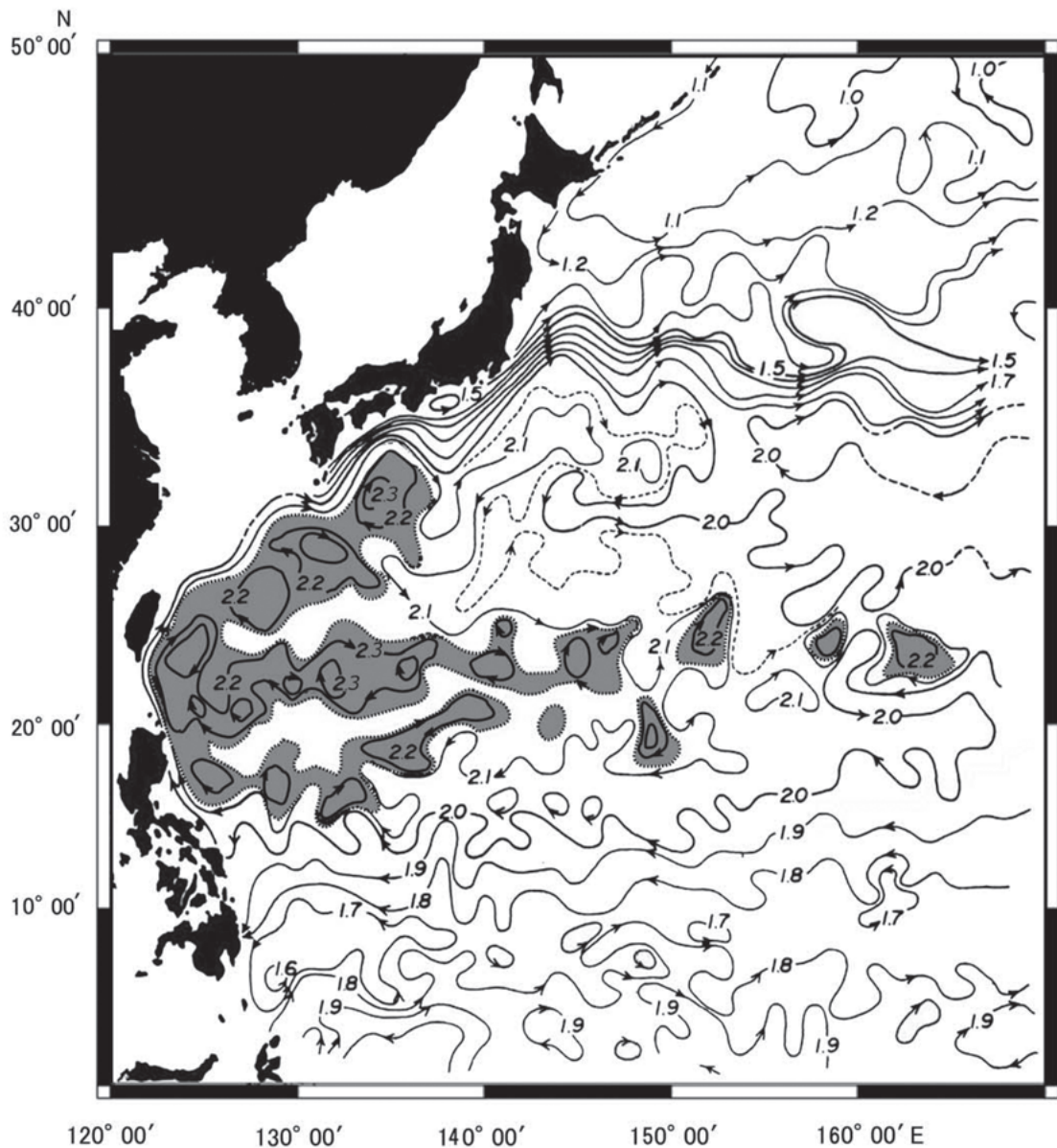


Fig. 5. Long-term mean geopotential anomaly at the sea-surface relative to the 1,000-db surface, in dynamic meters (from Hasunuma and Yoshida, 1978)

same spiny lobster species lives in both the Ryukyu and Ogasawara Islands, populations of the Ryukyu could be genetically isolated from those of the Ogasawara via IBD (the isolation by distance) effect. This is probably true for *P. longipes bicuspidatus* and *P. brunneiflagellum* (previously “Aka-ebi” type of *P. l. femoristriga* before Sekiguchi and George (2005);

The former inhabiting both the Ryukyu and the Ogasawara (but it is abundant in the Ryukyu while it is much less in the Ogasawara), while the latter is confined to the Ogasawara (Sekiguchi, 1991; Sekiguchi and George, 2005). In Taiwan, the other subspecies *P. l. longipes* is dominant whereas *P. l. bispinosus* is relatively rare. This suggests that populations of both

the Ryukyu and the Ogasawara might be genetically isolated from each other via the extension by the Kuroshio that flows northeast between northern Taiwan and southern parts of the Ryukyu. On the other hand, the fact that *P. japonicus* is not found in the Ogasawara may be explained by inefficient larval transport/supply of the species through the Kuroshio Subgyre because of the Ogasawara located south of the Kuroshio counter current (Sekiguchi, 1988).

Identification of phyllosoma and puerulus/nisto larvae in Japan and its neighbouring waters

Phyllosoma larvae: Phyllosomas have been identified using both direct and indirect methods. In the direct method, eggs hatched in captivity, or larvae caught at sea are cultured, sometimes to the puerulus/nisto stage. The indirect method, which is much less reliable, involves knowing palinurid and scyllarid species present as adults in the region where the larvae have been caught and deducing the probable phyllosoma identity based on adult distribution and abundance, while at the same time comparing morphological features of the larvae with those in published papers.

Phyllosomas collected to date in Japan and its neighbouring waters have been classified into three genera (*Linuparus*, *Panulirus*, *Puerulus*) of the Palinuridae, four genera (*Ibacus*, *Paribacus*, *Scyllarides*, and the previous genus *Scyllarus*) of the Scyllaridae, and one genus (*Palinurellus*) of the Synaxidae (Sekiguchi and Inoue, 2002). However, phyllosomas of three scyllarine species are absolutely dominant among the larvae collected in the waters (Sekiguchi, 1986a, b; Inoue *et al.*, 2001; Inoue and Sekiguchi, 2005): *Chelarctus cultrifer*, *Crenarctus bicuspidatus* and *Gelearctus kitanoviriosus*, the last of which is dominant in southern Japan and Taiwanese waters. *Scyllarine phyllosomas* are abundant in coastal waters, whereas *Panulirus* ones are often collected in offshore/oceanic waters (Inoue and Sekiguchi, 2005). Based on previous studies dealing with morphological features of phyllosomas to specific and generic levels (Sekiguchi and Inoue, 2002; Sekiguchi *et al.*, 2007), identification keys for phyllosomas of scyllarines and the *Panulirus* were compiled in Inoue and Sekiguchi (2006).

Puerulus/nisto stages: Nine *Panulirus* species/subspecies are found in Japanese waters (Sekiguchi, 2008): *P. brunneiflagellum*, *P. femoristriga*, *P. homarus homarus*, *P. japonicus*, *P. longipes bispinosus*, *P. ornatus*, *P. penicillatus*, *P. stimpsoni* and *P. versicolor*, of which *P. japonicus* is absolutely dominant, though *P. l. bispinosus* is found commonly in the Ryukyu while *P. brunneiflagellum* is found in Ogasawara Islands where the other five *Panulirus* species, except *P. japonicus* are reported, in the Ryukyu as well (Sekiguchi, 1991; Sekiguchi and George, 2005). Another three *Panulirus* species (*P. l. longipes*, *P. polyphagus*, and *P. stimpsoni*) are reported from Taiwanese waters (Sekiguchi and Inoue, 2002).

Molecular-based identification is most useful to unambiguously differentiate larvae when there are no obvious means to match adults with larval stages. The analysis of mtDNA for CO1 or 16SrRNA regions using universal primers allows the molecular characterization of an array of specimens that could belong to various phylogenetically distant taxa. To date, based on studies done by Chow (2006 a,b) molecular-based identification has been established in the western North Pacific to differentiate phyllosomas of *P. japonicus* from those of the other *Panulirus* species, particularly from *P. longipes* (*i.e.*, *P. brunneiflagellum*, *P. femoristriga*, *P. longipes longipes* and *P. l. bispinosus*).

Long distance larval transport and recruitment of *Panurilus japonicus* within the Kuroshio Subgyre circulation in the western North Pacific

A variety of scenarios may explain how recruitment to existing benthic populations eventually comes about, including (1) a proportion of hatched larvae are retained near adult populations within coastal waters, and latter recruit to them, with those larvae dispersing farther a field being destined to death because they end up in waters too deep or otherwise unsuitable for settlement and survival, and (2) larvae disperse widely offshore into oceanic waters, some returning shoreward by means of water circulation systems coupled with larval behavior that makes use of such systems.

An example of the first scenario is for the scyllarine species: Sekiguchi (1986) and Inoue and

Sekiguchi (2005) found that *Chelarctus* (previously *Scyllarus*, Holthuis, 2002) *cultrifer* phyllosomas that hatched along the Pacific coast of Japan and remained in coastal waters north of the Kuroshio contributed to recruiting to local benthic populations. In contrast, *C. cultrifer* phyllosomas that dispersed far offshore (into the Kuroshio Counter Current south of the Kuroshio) a long distance larval transport within the Kuroshio Subgyre circulation that also carries *P. japonicus* phyllosomas, Inoue and Sekiguchi (2001) may be destined to death because their larval duration is too short to allow them to return to coastal waters and there are currently no known populations of benthic juveniles and adults in the deep, offshore waters. In relation to coastal to offshore/oceanic processes, some behavioral traits of phyllosomas, such as long larval duration, different vertical

distribution/migration according to developmental stage, day/night and so on, may affect the transport/dispersal of the larvae. Scyllarine (previously the genus *Scyllarus*) species have a shorter larval duration of several months while *Panulirus* ones have a larval duration of nine months and more (Booth and Phillips, 1994; Sekiguchi *et al.*, 2007).

The early life history of *P. japonicus* can be summarized as follows (Sekiguchi, 1997): (i) the duration of phyllosomas is nearly nine months according to culture experiments by Kittaka and Kimura (1989) and Yamakawa *et al.* (1989). However, this estimate may be faster than for wild phyllosomas - (ii) first stage phyllosomas, released in summer, have been collected in coastal waters where berried females are found, (iii) benthic populations exist in waters under a strong influence

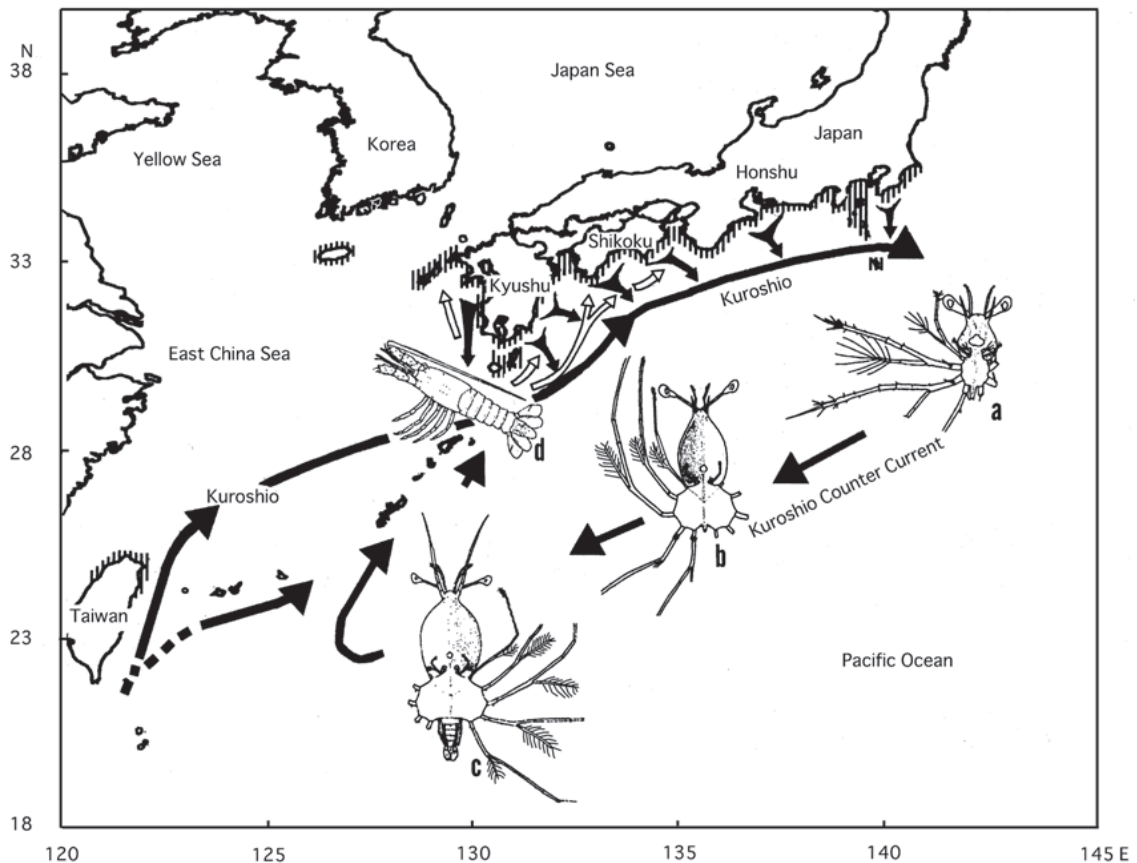


Fig. 6. Sekiguchi's hypothesis: schematic illustration of the larval transport of *Panulirus japonicus* within The Kuroshio Subgyre circulation (from Sekiguchi and Inoue, 2002). Areas with vertical lines: habitats of *P. japonicus* juveniles and adults, a, b, c and d: the early-, middle- and late-stage phyllosoma larvae, and puerulus stage of *Panulirus japonicus*

of the Kuroshio and its branches, (iv) phyllosomas in middle- to late-stages have rarely been collected in coastal waters inshore of the Kuroshio and (v) pueruli settle commonly and abundantly in coastal waters in summer. More recently, it was found that late-stage phyllosomas are found mainly in waters of south Kyusyu and also east of the Ryukyu, southern Japan (Yoshimura *et al.*, 1999; Inoue and Sekiguchi, 2001). Putting together the fragmentary information on the early life history of *P. japonicus* as related to the Kuroshio Subgyre circulation, Sekiguchi (1985, 1997) advanced a hypothesis to explain the larval recruitment processes that maintain *P. japonicus* populations in Japan and its neighbouring waters. Subsequently, this hypothesis was supported by direct evidence of Yoshimura *et al.* (1999) and Inoue and Sekiguchi (2001) as illustrated in Fig. 6.

Therefore, it is safe to say that phyllosomas and nistos of scyllarid species may be retained within coastal waters of west and north of the Kuroshio (Sekiguchi, 1986a; Inoue *et al.*, 2000, 2001; Inoue and Sekiguchi, 2001). Scyllarid phyllosomas are usually common and abundant in coastal waters, whereas *Panulirus* ones are often found in offshore/oceanic waters (Phillips *et al.*, 1981; Sekiguchi, 1986; Chiswell and Booth, 1999; Booth *et al.*, 2005). As indicated by Sekiguchi (1997), Inoue and Sekiguchi (2001) and Sekiguchi and Inoue (2002), the life history of *P. japonicus* may be completed within the Kuroshio Subgyre east and south of Japanese island and also east of Taiwan (Fig. 6), so that it takes nearly one year from egg hatching to settlement (this was also supported by rearing *P. japonicus* larvae by Kittaka and Kimura (1989) and Yamanaka *et al.* (1989)). Phyllosomas may be flushed out from coastal waters into the Kuroshio, transported through the Kuroshio Subgyre circulation south of the Kuroshio into the water of the east Ryukyu and Taiwan where they may attain subfinal/final-stage phyllosomas and pueruli, again entering the Kuroshio to disperse into the coastal waters.

Genetic population structure of *Panulirus japonicus*

Using allozymes and nucleotide sequence analysis of the mitochondrial DNA for the COI

region (cytochrome oxidase region I) and 16S ribosomal RNA genes (16S rRNA), the population structure has been examined for six species of spiny lobsters (including *P. japonicus*, Fig. 7).

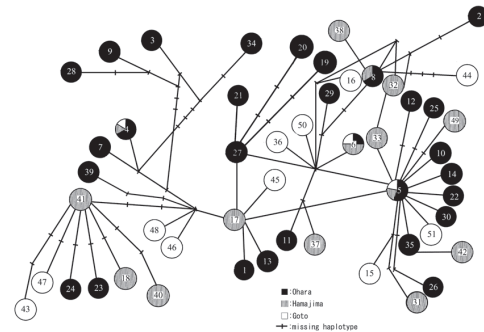


Fig. 7. The most parsimonious network for mtDNA haplotypes of *Panulirus japonicus* (from Inoue and Sekiguchi, 2007). Black, white, and vertical striped sectors: Relative frequencies of three distant locations (Ohara, Hamajima and Goto) in Japan where *P. japonicus* specimens (juveniles and adults) were collected. One section on the lines represents one missing haplotype. Ohara located in Chiba Prefecture, Hamajima in Mie Prefecture, and Goto in Nagasaki Prefecture (see Fig. 4 for locations)

Inoue *et al.* (2007) examined the population structure of *P. japonicus* using mtDNA for the COI region in order to test the hypothesis that benthic juveniles and adults are sustained by a population under a common pool of larvae. This study concluded that the *P. japonicus* is maintained from a common pool of long – lived phyllosoma larvae through larval transport within the Kuroshio Subgyre.

Panulirus japonicus populations regulated by larval supply variation coupled with the presence/absence of the large meandering path of the Kuroshio current

Previous studies of *P. japonicus* fisheries in Japan showed that it took 2-4 years following puerulus settlement in coastal waters for *P. japonicus* to recruit into fisheries resources (Yamakawa, 1997). Assuming that annual variation in *P. japonicus* catch may be determined by the variations in puerulus supply, and then that the puerulus supply may be affected by the presence/absence of the path of the Kuroshio, the annual variation in *P. japonicus* catch

may be closely related to oceanographic conditions in coastal waters 2-4 years earlier. This assumption was examined by Inoue and Sekiguchi (2009) using the data sets (Ministry of Agriculture of Japan) of the long-term annual variation in *P. japonicus* catch in Japan.

Two clusters (clusters A, B) were apparent in annual *P. japonicus* catch of different prefectures of Japan, cluster A is located east of Shionomisaki at the southern tip of the Kii Peninsula while cluster B is located west of the cape (Fig. 8).

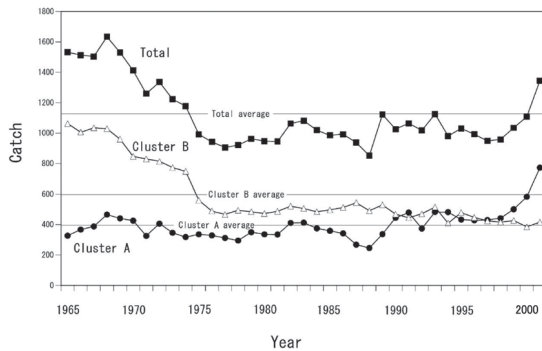


Fig. 8. Annual variation in *Panulirus japonicus* catch for two clusters (A, B) of prefectures in Japan (from Inoue and Sekiguchi, 2009). Cluster A includes six prefectures (*i.e.*, Wakayama, Kochi, Miyazaki, Kagoshima, Kumamoto, and Nagasaki), while cluster B includes three prefectures (*i.e.*, Mie, Shizuoka, and Chiba, see Fig. 4 for locations)

Based on the data between clusters A and B, three periods were distinguished with the first period the years before 1974, the second period the years from 1975 to 1989, and the third period the years from 1990 to 2001 (Fig. 9). For the first period, there was no significant relationship between these two clusters, whereas for the years from 1975 to 2001, a significantly negative relationship was detected. This finding suggests that although *P. japonicus* populations are sustained through a common pool of larvae as above-mentioned annual catch of *P. japonicus* in the waters west (cluster B) and east (cluster A) of Shionomisaki changed on a decadal scale.

There are previous few studies on annual variation in *P. japonicus* catch in Japanese waters (*e.g.*, Nonaka, 1982, 1988), but these studies did not identify multiple clusters of regions (Prefectures)

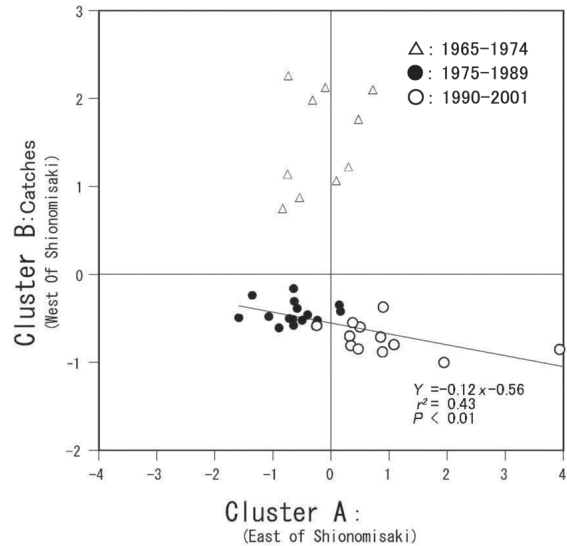


Fig. 9. *Panulirus japonicus* catch index between clusters A (east of the Cape Shionomisaki at the southern tip of the Kii Peninsula) and B (west of Shionomisaki) of prefectures in Japan depending on three regime periods (from Inoue & Sekiguchi, 2009). A regression model was fitted to combined data of periods 1975-1989 and 1990-2001

for annual catch variation and explained mechanisms causing annual variations. In contrast, by Inoue and Sekiguchi (2009), long-term trends in annual variation in *P. japonicus* catch were distinguished between west and east regions of Shionomisaki. These two clusters (A, B) corresponded to two clusters (a, b) of west and east capes of Shionomisaki using the shortest distance data from eight capes to the Kuroshio Current main axis, which may be related to the large meandering and the non-large meandering paths of the Kuroshio; West of Shionomisaki, the Kuroshio passed straight toward northeast along the continental shelf for each path, whereas east of the cape oceanographic conditions in coastal waters were markedly different between the large meandering and the non-large meandering paths of the Kuroshio (Kawabe, 1980).

These findings indicate that annual variation in *P. japonicus* catch in Japanese waters may be determined by variations in puerulus supply through the Kuroshio (*i.e.*, pre-settlement processes), not by post-settlement processes (including post-settlement mortality caused by fisheries).

Few studies in Japanese waters have been undertaken of seasonal/annual variations in puerulus supply and also in *P. japonicus* catch. Fishimi (1978) reported that the density of early juveniles of *P. japonicus* was higher in Shizuoka prefecture (cluster A in the above) east of Shionomisaki when the distance from the cape Irouzaki to the Kuroshio Current main axis was shorter than the year before. Based on frequent, short-interval surveys at sites of Shizuoka Prefecture using puerulus collectors for nearly 10 years from 1982 to 1991. Kawai *et al.* (1994) confirmed a higher puerulus supply of *P. japonicus* was significantly correlated with higher densities of early juveniles at year t+1 and also with higher catch at year t+2. This finding indicates that puerulus supply may be a key factory for determining annual variation in *P. japonicus* catch at a local scale (e.g., each prefecture in the above), and also at a larger spatial scale (e.g., two clusters of prefectures in the above).

Based on the NPI (North Pacific Index) that indicates normalized averages of sea surface air pressure in the North Pacific in winter (Trenberth and Hurrell, 1994), Aleutian low air pressure in the North Pacific became weaker during the first regime (years before 1976), was stronger during the second regime (years from 1977 to 1988) and was intermediate during the third regime (years from 1989 onward). This finding indicates that sea surface water temperature in the North Pacific became lower during the first regime and was higher during the second/third regimes, based on PDOI (Pacific Decadal Oscillation Index) that indicates annual averages of sea surface water temperature in the North Pacific (Trenberth and Hurrell, 1994). However, annual variations in winter NPI and also PDOI did not correspond to those in the KCI (including the presence/absence of the large meandering path of the Kuroshio, Inoue and Sekiguchi, 2009)). It remains unclear why relationships between the CI of clusters A and B varies depending not on KCI but on the three periods terminated by the regime shift.

Future research

Based on the above notion that the hypothesis explaining larval recruitment processes of *P.*

japonicus has been supported, the following three issues should be recommended for topics of future research: (i) mechanisms by which early-stage phyllosomas may be transported/flushed out into the Kuroshio from coastal waters inshore of the Kuroshio, (ii) mechanisms by which middle-stage phyllosomas may transfer from the Kuroshio to the Counter Current, and (iii) mechanisms by which subfinal/final-stage phyllosomas or pueruli may enter the Kuroshio from the waters of east Okinawa Islands and Taiwan. Unfortunately, we have no information on issues (ii) however, we have some information concerning issue (i), *i.e.*, *P. japonicus* phyllosomas are transported into the Kuroshio while scyllaridine ones are retained within coastal waters inshore of the Kuroshio (Inoue *et al.*, 2000, 2001). As related to the differences in larval duration between these two genera but with similar vertical distribution/migration to each other (Minami *et al.*, 2001), Sekiguchi (1997) predicted that most of early-stage phyllosomas of *P. japonicus* may be collected in the Kuroshio region around Hachijojima Island and neighbouring waters east of the Island, hence we may have a good chance to make clear the mechanisms by which early-stage phyllosomas are transported/flushed out into the Kuroshio from coastal waters.

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