Population dynamics and reproductive biology of the mysid *Orientomysis japonica* in Tango Bay, Japan

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Abstract: The mysids, *Orientomysis* spp., are common in shallow coastal waters and estuaries in Japan, and are reported to be one of the main prey items for juveniles of many commercially important fish species. Some studies have suggested that the seasonal dynamics of mysids are an important factor determining the biomass and production structure of demersal fish communities. In this study, seasonal variation in the population structure and reproductive traits of *Orientomysis japonica* Marukawa, 1928 were investigated in Tango Bay, the western part of Wakasa Bay, Japan, from April 2007 to April 2009. Mean densities at depths of 5 and 10 m were highest in spring (ca. 100 ind. m⁻²), decreasing drastically in early summer to nearly 0 ind. m⁻². Juveniles and immature individuals dominated the population (>80%) in spring and decreased in summer (<50%). Brooding females were captured year-round with mean body lengths ranging from 6.9 (August 2007) to 13.1 mm (February 2008). Body lengths of brooding females were negatively correlated with temperature. Brood size ranged from 1 to 102 and increased with female body length. The body sizes of all embryonic/larval stages within the marsupium were also negatively correlated with temperature. These results suggest that numerous large offspring released by the highly reproductive overwintering generation led to density increases and the maintenance of a high population density, while conversely, the summer–autumn generation exhibited repetitive short-term reproduction under high temperatures.

Key words: epibenthic mysid, *Orientomysis japonica*, reproductive trait, water temperature

Introduction

Mysids occur from abyssal to neritic sea areas worldwide and are especially abundant in coastal regions (Mauchline 1980). Because they are often the dominant marine benthic fauna in shallow waters, they are considered to be a key group in coastal food webs (Takahashi et al. 1999). Mysids have been reported to be one of the main prey organisms of many juvenile fish and carnivorous crustaceans in coastal areas (Oh et al. 2001, Link et al. 2002, Stergiou & Karpouzi 2002, Nakane et al. 2011), and to play an important role in the transport of primary products to organisms at higher trophic levels.

Large seasonal and interannual changes in the density of temperate mysids have been reported from estuaries and coastal waters (Wooldridge 1986, Fenton 1994, Mees et al. 1994, Sudo et al. 2011) and these changes probably affect production and the year-class strength of fishes (Feyrer et al. 2003).

Many species of temperate, shallow-water mysids have two major generation types: the cold-season generation, which is long-lived and grows to a large size; and the warm-season generation, which is small and short-lived (Mauchline 1980). The body size, brood size (number of embryos/larvae within a marsupium), and egg size of mysids vary seasonally in association with the generation type (Hanamura 1999, Takahashi & Kawaguchi 2004). Seasonal changes in the ecological traits of mysids may have a large influence on the total productivity of the population. Information on the growth, reproduction, life span, alternation of generations, and their responses to various environmental factors are important for understanding mysid population dynamics and the mechanisms leading to
variation in these dynamics.

Some detailed results have been reported from laboratory-rearing experiments, examining the growth and reproduction of mysid species (Clutter & Theilacker 1971, Toda et al. 1984, Yamada & Yamashita 2000, Ma et al. 2001, Winkler & Greve 2002, Sudo 2003, Fockey et al. 2005). In those studies, water temperature was concluded to be the most important abiotic factor affecting seasonal changes in population dynamics including growth rate, intermolt period, molt increment, age at maturity, brood size, and the size and incubation time of brooding females (Yamada & Yamashita 2000, Sudo 2003).

Orientomysis japonica Marukawa, 1928 (often reported as Acanthomysis japonica and as a synonym of A. nakazatoi; see Fukuoka & Murano 2005) is an epibenthic mysid distributed throughout the coastal waters of Japan at depths shallower than 10 m (Ii 1964, Hirota et al. 1989, Fukuoka & Murano 2005). This species dominates the mysid community in Tango Bay, the western part of Wakasa Bay in the Sea of Japan, and is one of the main food items of juvenile Japanese flounder Paralichthys olivaceus (Temminck & Schlegel, 1846), temperate seabass Lateolabrax japonicus (Cuvier, 1828), and sand shrimp Crangon uritai Hayashi & Kim, 1999 (Minami 1982, Fuji et al. 2010, Antoni et al. 2011).

No information on the growth, survival, and reproduction of O. japonica have hitherto been available, although this species plays an important role in sandy ecosystems around Japan. This species is also considered to be susceptible to variation in water temperature because of its occurrence in the temperate zone. In the present study, seasonal variation in the density, size, and maturity of O. japonica in the field were investigated, as well as patterns of variation in its breeding traits and reproductive structures, also considering the effects of ambient temperature. Particular focus is placed on breeding trait characteristics, such as the sizes of brooding females, broods, and embryos/larvae.

Materials and Methods

Field sampling

The study site was a shallow area of Tango Bay, which is a semi-open bay located in the western part of Wakasa Bay, into which the Yura River empties (Fig. 1). The annual average discharge of the Yura River is 51.5±10.2 m³ s⁻¹ (mean±SD, from 2001 to 2010; Ministry of Land, Infrastructure, Transport and Tourism, Japan, 2015). However the discharge of Yura River water is reported to affect only the salinity of the surface layer, because the Yura Estuary is classified as a weakly mixed, microtidal estuary (Kasai et al. 2010), so the annual variation in the salinity of the bottom layer is considered to more closely reflect the salinity of the offshore water. The bottom substratum was largely composed of fine-grained sand (mean of median particle diameters, Mdϕ: 225 μm, 160 μm) at depths of 5 m and 10 m, and very fine-grained sand (Mdϕ: 90 μm) at a depth of 20 m, moderately sorted (Folk & Ward 1957) at each depth (mean of degree of sorting, σI: 0.63, 0.55, 0.74).

Mysids were collected monthly during the day with an epibenthic sledge net. From April to November 2007, the mesh size was 20 cm H, 30 cm W, 500 μm mesh; and from December 2007 to April 2009 40 cm H, 30 cm W, 500 μm mesh (the first net was lost during field sampling). The catch efficiencies of these two nets in terms of unit area are considered to be identical. Two-story net sampling (20 cm + 20 cm H, 30 cm W, 500 μm mesh) confirmed that O. japonica is distributed less than 20 cm off the bottom in the daytime (Akiyama, unpublished data). Three one-minute net tows along the shoreline (tow speed ca. 2 knot) were replicated three times at a depth of 5 m from April to December 2007; and at depths 5, 10, and 20 m from January 2008 to April 2009 (Fig. 1). The towing distance (61.6±13.1 m) was calculated based on the recording of latitude and longitude positions from a global position-
Table 1. Allometric equations used to estimate body length and weight of Orientomysis japonica using linear and power regressions.

| Parameters (mm) | Constants | Regression equation | $r^2$ | n  | p  |
|----------------|-----------|---------------------|-------|----|----|
| $CL$ (carapace length) | $BL$ (body length) | $y=ax^b$ | 0.936 | 150 | <0.001 |
| $TL$ (telson length) | $BL$ | $y=ax^b$ | 0.931 | 150 | <0.001 |
| $ExL$ (exopod length of uropod) | $BL$ | $y=ax^b$ | 0.925 | 150 | <0.001 |
| $EnL$ (endopod length of uropod) | $BL$ | $y=ax^b$ | 0.936 | 150 | <0.001 |
| $BL$ | $WW$ (wet weight) | $y=ax^b$ | 0.947 | 150 |       |
| $BL$ | $DW$ (dry weight) | $y=ax^b$ | 0.948 | 150 |       |

$BL$: body length (mm), $CL$: carapace length (mm), $TL$: telson length (mm), $ExL$: exopod length of uropod (mm), $EnL$: endopod length of uropod (mm), $WW$: wet weight (mg), $DW$: dry weight (mg).

Measurements

In the laboratory, all mysids were sorted and identified. For each species of mysid, the number of individuals was counted and the total wet weight of individuals was recorded. The annual mean density and biomass of mysids at each depth were calculated from January 2008 to April 2009. The mean value of two years was used for January, March, and April in this calculation, because there were two years’ data for these months. Approximately 100 randomly selected $O. japonica$ individuals from each month’s sample were separated into four categories (brooding females, mature females, mature males, and immature individuals) according to Mauchline (1980), and their carapace length ($CL$: length from apex of rostrum to posteromedian margin) was measured. Females with the marsupium fully developed, but not yet filled with young, were classified as mature; and mature females with young present in the marsupium were classified as brooding females. All brooding females were separated from the collected samples and counted. Their $CL$ and brood size (the number of embryos/larvae in a marsupium) were measured. Here, the term ‘embryo’ designates an individual before hatching from the egg membrane, while ‘larva’ refers to a post-hatching individual in the marsupium. Embryonic and postembryonic development in the marsupium was divided into three stages based on the following morphological criteria (Mauchline 1980):

Stage I: egg-like embryo.
Stage II: comma-shaped larva hatched from the egg membrane.
Stage III: post-molt larva with eyestalks.

From 1 (January 2009) to 173 brooding females (April 2009) were obtained from each month’s sample, and five embryos/larvae were selected at random from the marsupium of each female. The body length of intra-marsupial larva (stage II & III) was defined as a sum of lengths from the anterior end of the body except eyes to the bend of the body and from that to the posterior end. The diameter of embryo and the body length of larva were measured under a binocular microscope with an ocular micrometer. Embryo/ larval size was defined as the mean diameter/body length of the five embryos/larvae from each female. Some species of mysids occasionally adopt abandoned larvae (Wittmann 1978, Sato & Murano 1994, Wortham-Neal & Price 2002), and in this study, one brooding female with stage I embryos was found to have adopted one stage III larva: this female was recorded as holding stage I embryos.

To calculate the standard body length ($BL$; from the anterior end of the rostrum to the end of the last abdominal segment) and the wet/dry weight ($WW/DW$) of $O. japonica$ in every developmental stage except embryo/larva in the marsupium, allometric equations were developed using linear and power regressions (Table 1). For 150 randomly selected individuals collected in April 2008, $BL$ and the length of body parts such as the carapace, telson, and uropods were measured using a microscope with a profile projector (V-12: Nikon Corporation, Tokyo, Japan). The wet weight of the mysid body was measured after moisture absorption on a paper towel for 2 min, and the dry weight of the same individual was measured after drying in an oven at 60°C for 48 h.

Results

Hydrographic conditions

The temperature at the seabed ranged from 11.1°C to 28.5°C during the sampling period (Fig. 2a). No significant difference in temperature was observed among the depths of 5, 10, and 20 m (one-way repeated measures ANOVA, $p>0.05$). Salinity also showed seasonal change (Fig. 2b), with a maximum salinity (34.3) observed in June and a minimum (32.5–32.8) occurring in March and August.
Seasonal changes in the occurrence, distribution, size, and stage composition of *Orientomysis japonica*

Estimated annual mean density (among 15 mysid species collected in the sampling area) of *O. japonica* was 76.4% (the most abundant) of all mysids at the shallowest depth (5 m); 30.7% (second in abundance) at 10 m; and 0.2% (scarce) at 20 m (Fig. 3). This species ranked only second at 10 m because of the dominance of *O. rotundicauda* (Liu & Wang, 1980) in January 2008. If these January data are excluded, *O. japonica* accounted for 38.4% of the mysid community and achieved dominance at 10 m. At 5 and 10 m, *Nipponomysis* spp. and *Archaeomysis japonica* Hanamura et al., 1996, were the second most abundant species after the *Orientomysis* mysids; and *Mysidopsis japonica* Ii, 1964, and *Rhopalophthalmus orientalis* Tattersall, 1957, dominated the mysid community at 20 m.

In 2008, the annual mean density and biomass of *O. japonica* were, respectively, 43.2±72.3 ind. m$^{-2}$ (mean±SD) and 135.9±246.0 mg WW m$^{-2}$ at 5 m, and 19.5±36.9 ind. m$^{-2}$ and 138.3±213.1 mg WW m$^{-2}$ at 10 m (Fig. 4). Sampling at 20 m was only performed in April 2009 (0.3±0.6 ind. m$^{-2}$). The mean density and biomass at 5 and 10 m were highest in spring (about 100 ind. m$^{-2}$, 300 mg WW m$^{-2}$; February–May), and decreased substantially in early summer (June, July) to almost zero in September and October.

There were no significant differences in BL between mature males and females (brooding females+mature females) (two-way repeated measurements ANOVA with sex and sampling date, $p=0.19$), but sampling date and the interaction between sex and sampling date were significant ($p<0.001$; $p=0.003$). In summer months, when less than 10 mature males and females were caught, this comparison was not made. The body size of mature mysids was large from January to May with a range of 8–16 mm BL, and then rapidly decreased to 6–11 mm BL in June, remaining small to October. BL gradually increased in November and
Fig. 5. Size frequency distributions of *Orientomysis japonica* from April 2007 to April 2009 at a depth of 5 m. *n* indicates the number of individuals measured; when *n*<90, the carapace lengths of all collected individuals were measured.
December (Fig. 5).

The ratio of immature individuals sampled at 5 m varied with season, ranging from 21.8% to 92.3%. In spring, immature mysids dominated the population (>80%), but their abundance decreased in summer (<30%) at 5 m (Fig. 5, 6). In samples collected from 10 m, the tendency was similar to the samples at 5 m, but the percentage of large individuals was somewhat higher than that at 5 m in winter and spring when population size was large (Fig. 7). The sex ratio (male/female) of *O. japonica* ranged from 0.0 to 4.0 (median: 1.18), but there were no significant differences (male : female=1 : 1) (binomial test, p>0.05 for each month) and no distinct seasonality. Four months indicated more than 2.0 or less than 0.5 in the sex ratio, when the number of individuals used in sexual distinction ranged from 1 to 14 because only a small number of individuals were collected (cf. Fig. 5).

### Reproductive traits of females

The density of brooding females displayed similar seasonal changes to that of the whole population (Figs. 4, 8): it was highest in June 2007 (2.1±1.0 ind. m⁻²) and April 2008 (1.7±1.2 ind. m⁻²); and lowest in summer (nearly 0 ind. m⁻²) at 5 m. In contrast, the incidence of brooding females was low in spring (approximately 5%), increased in summer (e.g., 20.5±18.6% in September 2007, 47.6±45.9% in July 2008), and then decreased in autumn–winter (Fig. 8). In other words, the population density and incidence of brooding females was inversely related.

The body length of brooding females increased moderately from autumn to late spring and decreased rapidly in summer (Fig. 5). Monthly mean BL was maximum in February 2008 (13.16±0.66 mm) and minimum in August 2007 (6.94±0.42 mm). A clear negative relationship was observed between the BL of brooding females and water temperature, as expressed by the following equation (Fig. 9):

\[
MBL = \frac{244.45}{(T + 6.64)^{0.67}} \quad (r^2 = 0.67, n=859) \quad (1)
\]

where *MBL* is the maternal BL (mm), and *T* is the water temperature (°C) at the time of sampling. The BL of

![Fig. 6. Abundance (density) of different size classes of *Orientomysis japonica* at a depth of 5 m.](image)

![Fig. 7. Life stage composition of *Orientomysis japonica* from April 2007 to April 2009. (a) 5 m, (b) 10 m and (c) 20 m depth. *, no mysids. For key, see legend of Fig. 5.](image)

![Fig. 8. Density and percentage of brooding females of *Orientomysis japonica* at a depth of 5 m from April 2007 to April 2009. (Vertical bars indicate SD). *, no mysids; **, no brooding females.](image)

![Fig. 9. Relationships between water temperature and maternal body length in *Orientomysis japonica*.](image)
Population dynamics of *Orientomysis japonica*

Brooding females decreased with increasing temperature. The relationships between the diameter of embryos or the length of larvae in the marsupium and MBL are given by the following equations (Fig. 10a):

Stage I \[ L_{S_1} = 0.015MBL + 0.35 \ (r^2 = 0.50, n = 218) \]  
Stage II \[ L_{S_2} = 0.047MBL + 0.70 \ (r^2 = 0.53, n = 303) \]  
Stage III \[ L_{S_3} = 0.071MBL + 0.80 \ (r^2 = 0.57, n = 130) \]  

where \( L_{S_k} \) is the diameter of embryos or the length of larvae (mm) of stage \( k \). Larger females generated larger offspring. The correlations of the diameter of embryos and the length of larvae in the marsupium with water temperature are expressed by the following equations (Fig. 10b):

Stage I \[ L_{S_1} = 27.07(T + 37.49) \ (r^2 = 0.54, n = 218) \]  
Stage II \[ L_{S_2} = 39.42(T + 17.10) \ (r^2 = 0.65, n = 303) \]  
Stage III \[ L_{S_3} = 52.60(T + 17.75) \ (r^2 = 0.67, n = 130) \]  

The diameter of embryos and the body size of larvae were smaller at higher temperatures.

Because many brooding female peracarid crustaceans lose embryos/larvae from the marsupium during net collection and laboratory sorting (Wägele 1987, Murtaugh 1989), it was difficult to determine an accurate brood size. Therefore, the relationships between mean or maximum brood size and MBL were estimated as follows (Fig. 11):

\[ BS = 0.07MBL^{2.33} \ (r^2 = 0.28, n = 651) \]  
\[ BS_{\text{max}} = 0.06MBL^{2.72} \ (r^2 = 0.91, n = 26) \]  

where \( BS \) is the mean brood size (ind.\(^{-1}\)) and \( BS_{\text{max}} \) is the maximum brood size (ind.\(^{-1}\)). Larger *O. japonica* females tended to have more eggs, with a 15.3-mm-long female having the largest brood (102). The maximum densities of embryos/larvae in the marsupium in the wild at a depth of 5 m were calculated using \( BS_{\text{max}} \). The density of embryos/larvae in the marsupium increased in autumn and was higher than the population density from November to January, just before the population density began to increase rapidly (Fig. 6).
Seasonal changes in population structure

The results suggest that water temperature is the main factor affecting the reproductive traits and population dynamics of *O. japonica*. The seasonal change in population dynamics revealed in this species is also thought to be associated with a change in temperature.

In *O. japonica*, body size and size at brooding were larger in seasons with low temperatures. In particular, the BL of brooding females was largest in winter–spring and smallest in summer (Fig. 5), and was therefore very much related to temperature (Fig. 9). In other *Orientomysis* mysids, such as *O. robusta* (Murano, 1984) and *O. mitsukurii* (Nakazawa, 1910), reared under temperature-controlled conditions, the intermolt period, life span, body size, and size at maturity (or size at brooding) were reported to be negatively correlated with temperature (Yamada & Yamashita 2000, Sudo 2003). Occurrences of a large overwintering generation and a small summer generation found in *O. japonica* agree with the general traits of mysid species in mid-latitude regions (Mauchline 1980).

Within mysid species, larger individuals generally produce more, and larger, eggs (Saltzman 1996). Therefore, because females are larger at lower temperatures, brood size and egg size also tend to be larger at lower temperatures (Murano 1964, Toda et al. 1982, Yamada & Yamashita 2000). In the present study, the brood size of *O. japonica* ranged from 1 to 102 individuals, similar to that of *O. robusta* (6–122 ind.; Sudo et al. 2011). In line with previous findings (Kajikawa 1978), larger females had more eggs (Fig. 11), with a female of BL 15.3 mm having the largest brood size of 102 individuals. Larger females also produced larger eggs and larvae at lower temperatures (Fig. 10). Because the production of multiple broods is common in mysid species (e.g., Fenton 1994, Hanamura 1999, Lejeunes & Chevaldonné 2005), and the maximum number of spawns per lifetime is reported to be four for *O. robusta* (Sudo 2003) under laboratory conditions, it is likely that *O. japonica* produces multiple broods.

It is common for mysid species in mid-latitude temperate regions to have a large overwintering generation, which is born in late autumn and survives until spring; and a small summer generation (Mauchline 1980). In the present study, the winter–spring generation had a large body size, high biomass, and high numbers of embryos/larvae, juveniles, and adults; while the summer–autumn generation was characterized by a low density, small adult size, and few embryos/larvae.

Larger mysids began to appear with the upturn in population abundance in November (Fig. 5). The maximum lifespan of *O. robusta* at 10–15°C under laboratory conditions is reported to be 128–223 days (Sudo 2003). Assuming the lifespan of *O. japonica* to be equal to that of *O. robusta* (in light of the autumn and winter water temperatures and the comparable body sizes of both mysids), individuals produced from November onward are likely to represent the overwintering generation. It is notable that the density of embryos/larvae increased first, followed by increases in juveniles and adults (Fig. 6). Given that larger larvae are likely to survive better (and that the large brooding females occurring at low temperatures have high fecundity and produce large embryos), the reproductive capability of *O. japonica* seems to be maximized in winter–spring, leading to a high abundance of mysids during this season. In addition, the occurrence of a phytoplankton bloom from February to May (Watanabe, submitted) in Tango Bay might support mysid production, although information regarding the feeding habits of *O. japonica* is limited.

The population density of *O. japonica* declined sharply in June–July when temperatures were around 20°C. Decreased reproductive capability (due to decreases in the size of brooding females and survival rate of newly hatched juveniles with increased temperature) is thought to be an important factor in forming the summer–autumn generation. The mortality rate of juveniles of the temperate *Neomysis awatschensis* (Brandt, 1851) (reported as *N. intermedia*) was reported to increase at higher temperatures (Toda & Takahashi 1985). The optimal temperature for survival and growth of *O. japonica* has not been studied, but the summer–early autumn temperature range in Tango Bay is thought to be suboptimal: the summer–autumn population had an extremely low density, indicating that they survived (but in low numbers) under environmental conditions of high temperature and low primary productivity during this season. The maximum lifespan of *O. robusta* at 20–25°C under laboratory conditions is reported to be 40–63 days, and the age at first maturity decreases with increasing temperature (Sudo 2003). This suggests that the summer–autumn generation of *O. japonica* undertakes repetitive short-term reproduction with short life span during the high-temperature period.

*Xenacanthomysis pseudomacropsis* (Tattersall, 1933) (reported as *Acanthomysis pseudomacropsis*) has been reported to undergo seasonal horizontal migrations (Morioka & Takahashi 1980) between shallow coastal areas and deep areas (250–300 m depth). However, it is unlikely that the seasonal changes in the density of *O. japonica* observed in the present study were caused by this kind of nearshore–offshore migration, because very few *O. japonica* were collected at depths >20 m in Tango Bay throughout yearly sampling (Fig. 4, Antonio et al. 2010, Antonio et al. 2012). Concerning areas shallower than 5 m, Aoki et al. (2014) conducted monthly sampling using a plankton sledge net at a site of 1 m depth near to the present study area and *O. japonica* was not collected (Aoki pers. com.). The estimated smallest BL of free swimming juveniles (1.3–2 mm; Fig. 10) was smaller than that of juveniles collected (ca. 3 mm; Fig. 5). This indicates that newly released larvae were not caught in the present study. The distribution area and depth
zone of these small, newly released larvae are unknown.

**Ecological significance of mysid population dynamics**

Juvenile temperate seabass and Japanese flounder use the shallow coastal waters of Tango Bay from April to autumn as a nursery ground and mainly consume mysids (Maeda 2002, Fuji et al. 2010, 2011, Islam et al. 2010, Takeno 2010). Because the juveniles of both of these fishes prefer epibenthic to sand-burrowing mysids as prey items (Hirota et al. 1990, Fuji et al. 2010, Takeno 2010), *O. japonica* is likely to be the dominant prey for the juveniles of these two commercially valuable fish in this area. However, the maximum density of *O. japonica* recorded in this study ranged from 100 to 200 ind. m$^{-2}$, which is lower than the density of *O. mitsukurii* in the Pacific coastal waters of Tohoku district in northeastern Japan (1,000–2,500 ind. m$^{-2}$) and *O. robusta* of the Japan Sea off Igarashi Beach, Niigata Prefecture (about 1,000 ind. m$^{-2}$; Yamada et al. 1994, Sudo et al. 2011). Fuji & Noguchi (1996) reported that the growth rate of wild Japanese flounder increased with mysid density and reached satiation at 100–150 ind. m$^{-2}$. The maximum density of *O. japonica* in the study area was similar to this satiation density and a rapid decrease in mysid density in early summer coincided with the period when requirement of juvenile fishes on mysids was estimated to be largest. Therefore, both mysid abundance and the timing of the decrease in mysid density are thought to affect the survival rates of Japanese flounder and temperate seabass juveniles more strongly in this area than in the northern Sea of Japan and the Pacific coast of Tohoku, where density of mysids sufficient to raise juvenile fish populations is maintained for long periods.

Off the Japan Sea and the Pacific coasts of Tohoku, the market return rate of hatchery-raised Japanese flounder released for stock enhancement is significantly higher than in other areas (Yamashita & Aritaki 2010). This can be attributed to differences in the scale of the excess capacity of mysids, which can be consumed by fishes released in coastal areas. Therefore, mysid productivity in Tango Bay is unlikely to be able to maintain stocks of hatchery-raised fishes.

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