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Research Article

Role of temperature in the reproductive cycle of *Thais chocolata* (Gastropoda, Muricidae) in Chanavaya, Tarapacá, Chile

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ABSTRACT. The reproductive condition of *Thais chocolata* (copulative aggregation establishment, clutch laying in capsules and specimen density), was studied monthly between February 2009 and January 2010, in the locality of Chanavaya (Tarapacá, Chile). Results showed that the specimens are mainly distributed in aggregations, and that their gonad development is asynchronous with the presence of mature females being registered during the entire year. Reproductive aggregations were found in the shallow stratus from late January to August 2009 and reappearing in January 2010. However, the larger ones (which sustained extraction) occurred during June-July and January. An increase in specimen density in the 5 to 17 m stratum was registered in May-August and December-January, coinciding with the periods previous to, during and after the highest aggregation magnitudes registered. The aggregation periods coincided with temperatures over 15°C, with a lower reproductive activity associated to a decrease in temperature. We state that abrupt temperature changes occurring in short time periods could cause mature specimen to move, increasing their density in shallow waters for reproductive purposes. We suggest increasing protection for the resource during the reproductive aggregation processes given that extraction leaves the clutches unprotected and prone to predation from other organisms.

Keywords: *Thais chocolata*, gastropod, reproduction, aggregation, temperature, Chile.

Rol de la temperatura en el ciclo reproductivo de *Thais chocolata* (Gastropoda, Muricidae) en Chanavaya, Tarapacá, Chile

RESUMEN. La condición reproductiva de *Thais chocolata* (establecimiento de agregación copulativa, postura de cápsulas y densidad de especímenes), se analizó mensualmente entre febrero de 2009 y enero de 2010, en la localidad de Chanavaya (Tarapacá, Chile). Los resultados, mostraron que los ejemplares se distribuyen principalmente agregados, y que su desarrollo gonadal es asincrónico, con presencia de hembras maduras durante todo el año. Se encontraron agregaciones reproductivas en el estrato somero desde fines de enero hasta agosto de 2009, reapareciendo en enero de 2010. Sin embargo, las mayores magnitudes (que sustentaron su pesquería), ocurrieron durante junio-julio y enero. Se registró un incremento en la densidad de ejemplares en el estrato de 5 a 17 m de profundidad en mayo-agosto y diciembre-enero, coincidentes con aquellos en los que se desarrollaron las mayores agregaciones. Los periodos de agregaciones masivas, coincidieron con periodos de temperaturas mayores de 15°C, disminuyendo la actividad reproductiva con la temperatura. Se postula que variaciones bruscas de temperatura que ocurren en cortos periodos de tiempo, podrían causar que los especímenes maduros se desplacen, aumentando su densidad en aguas someras para reproducirse. Se sugiere proporcionar mayor protección al recurso durante su proceso de agregación reproductiva, dado que su extracción deja las posturas desprotegidas y propensas a la depredación por otros organismos.

Palabras clave: *Thais chocolata*, gasterópodo, reproducción, agregación, temperatura, Chile.

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INTRODUCTION

Thais chocolata (Duclos, 1932) is a mollusk found between Paita, Perú, and the Valparaíso region in

Chile (Osorio, 2002). Historically it has been an important benthic resource for artisanal fishing economy in northern Chile. However, given the high exploitation levels since 1978, and after reaching the

maximum catch level in 1986 with 8,244 ton (Avendaño *et al.*, 1998), the vulnerable fraction of the shallow area strongly decreased. Extraction of *T. chocolata* is currently restricted to the Arica and Parinacota, Tarapacá, and Antofagasta regions, where in 2010 only 160 ton (SERNAPESCA, 2010) were extracted, corresponding to the lowest catch level since the beginning of the resource's exploitation.

This snail is distributed in depths between 5 and 40 m, over rocky and shell substrates and over thick sand (Andrade *et al.*, 1997; Avendaño *et al.*, 1997, 1998). It is a gonochoric species, with internal fertilization and without external evidence of sexual dimorphism (Rojas *et al.*, 1986). During the reproduction season, adults concentrate forming aggregations (Retamales & González, 1982; Avendaño *et al.*, 1997, 1998), as occurs with other species of this genus (Bertness, 1977; Palmer, 1983). This strategy, in which adult specimens group together during reproductive seasons, has serious consequences for their survival, given that fishers resort mainly to these aggregations for extraction (Andrade *et al.*, 1997; Avendaño *et al.*, 1997, 1998). In Chile, closed seasons have been established with fixed extraction periods to protect the reproductive activity. However, the few studies concerning the reproductive cycle (Andrade *et al.*, 1997; Avendaño *et al.*, 1997, 1998), and which currently sustain this closed season, showed that the species does not present a specific reproduction season, with mature specimen being present the entire year, and showing certain increases in presence during some months. Clutches can also be observed during most of the year, invalidating the establishment of fixed extraction periods. These studies have also shown that sexually immature females are frequently found in deeper areas, while mature specimens tend to be found in more shallow waters (Retamales & González, 1982; Rojas *et al.*, 1986; Andrade *et al.*, 1997; Avendaño *et al.*, 1997, 1998).

There is little information concerning exogenous factors acting on the reproduction processes of this species, considering that temperature and feeding have been proven to be the most influential factors on the reproductive cycles of mollusks (Peña, 1987; Román *et al.*, 2001; Michel-Morfin *et al.*, 2002; Ponce-Díaz *et al.*, 2003). With the objective of showing whether the reproductive process of this species responds to environmental temperature variations, in the present study we have monitored the reproductive cycle of this gastropod, its distribution between 5 to 20 m depth, and the temperature of the deep section of an exposed area in the Tarapacá region, Chile.

MATERIALS AND METHODS

The study area is located in Chanavaya (20°53'S, 70°08'W), Tarapacá region, Chile. In this area *T. chocolata* is distributed over a rocky substrate, associated in the shallow areas with banks of the mytilidae *Choromytilus chorus* (Molina, 1782), and the brown algae *Lessonia trabeculata* (Villouta & Santelices, 1986), and in the deep area, with banks of the mytilidae *Aulacomya ater* (Molina, 1782) which extends over 30 m depth. This area is located in a subtropical transition zone, with predominance of the Subantarctic Water mass (SAAW), which dominates the upper 200 m of the northern branch of the cold Humboldt Current System. These waters (SAAW), mix with a lower proportion of Subtropical waters with greater salinity and temperature, and also periodically mixed with colder Equatorial Subsurface waters from greater depths, which rise to the coast given upwelling processes induced by south and southwest winds that predominate in the area (Avendaño & Cantillán, 2008).

A data loggers (model Tid Bit, onset), programmed to register temperature measurements every hour, starting February 2009 through January 2010, was installed in the study area at 16 m depth, with the objective of evaluating the potential role of temperature in the reproductive process of *T. chocolata*.

Between early February 2009 and January 2010, random monthly samplings between 5 and 20 m depth were carried out by diving, to determine the distribution of *T. chocolata* through density (20 m is the authorized limit for compressor diving, used by mollusk divers in the extraction of benthic resources in Chile (Armada de Chile, 2006)). For this purpose, three sampling transects were marked using a GPS map 76CSx Garmin. These transects were separated by 100 m from each other and covered both isobaths. In each one of these transects, the specimen density was determined randomly, dropping a 1 m² quadrant and replicating it 10 times along said transect. On each sampling point, the depth was registered using a Beuchat CX 2000 comex submarine computer.

The resource distribution model was characterized using the Morisita Dispersion Index (1962), reinforced using the Standardized Index (Smith-Gill, 1975), which acts independently of studied population density and sample size (Myers, 1978). The Standardized Index turns the values of the original index into an absolute scale varying between -1 and +1, with a confidence interval between +0.5 and -0.5 at $\alpha = 0.05$. For this index, random patterns mark 0, values above 0 represent aggregated distributions and values below 0 correspond to a uniform distribution pattern.

A submarine route was followed to detect the presence of *T. chocolata* reproductive aggregations, covering a distance of 300 m parallel to the coastline between 5 to 17 m depth. The reproductive cycle of *T. chocolata* was studied from a monthly sample of 40 specimens over 30 mm of maximum length, extracted from the three sampled transects. An additional sample of 25 specimens was added every time reproductive aggregations were found. The extracted specimens were transported to the laboratory where they were dissected and sections of the middle area of the gonad–hepatic gland complex of 100% of the females (considering that they better represent the reproductive processes (Cantillán et al., 2011)), were fixed in Bouin and included in paraffin. Cuts 6 μ m thick were colored with hematoxylin and eosin (Gabe, 1968), and were then microscopically analyzed to classify their maturity state, according to the scale proposed by Cantillán et al. (2011).

RESULTS

During the period of study, the average daily temperature, registered at 16 m depth, varied between 13.6 and 16.8°C (Fig. 1a). During May, June, July, and December 2009 and January 2010 the average monthly temperature rose above 15°C, while a strong decrease was registered during April 2009, the coldest month, with an average of 13.8°C (Fig. 1b).

The density of *T. chocolata* in the sampled strata varied between 0 and 27 ind m^{-2} , presenting an aggregate distribution according to the Morisita Index (Table 1). Considering this aggregated distribution, the average monthly abundance was determined from the quadrants with a registered presence of specimens, within the stratus in which reproductive aggregations were found (5 to 17 m depth). The results obtained using this criteria showed important specimen abundance increases during June–August, with averages between 10.1 and 8.4 ind m^{-2} , and during December–January, with averages of 9.0 and 14.0 ind m^{-2} , respectively (Fig. 2).

The reproductive stages of female *T. chocolata* in the samples showed that maturity was present during the entire year, in proportions varying between 45.7 and 83.9%, with the highest levels registered in May 2010 (Fig. 3). Specimens with evacuated gonads (fluctuating between 3.0 and 42.9% of the sample), were registered during the entire study period except in April and May (Fig. 3). The integration of both reproductive stages (mature and evacuated), showed that the highest percentages occurred during July–August with 85.2 and 88.6% of the population,

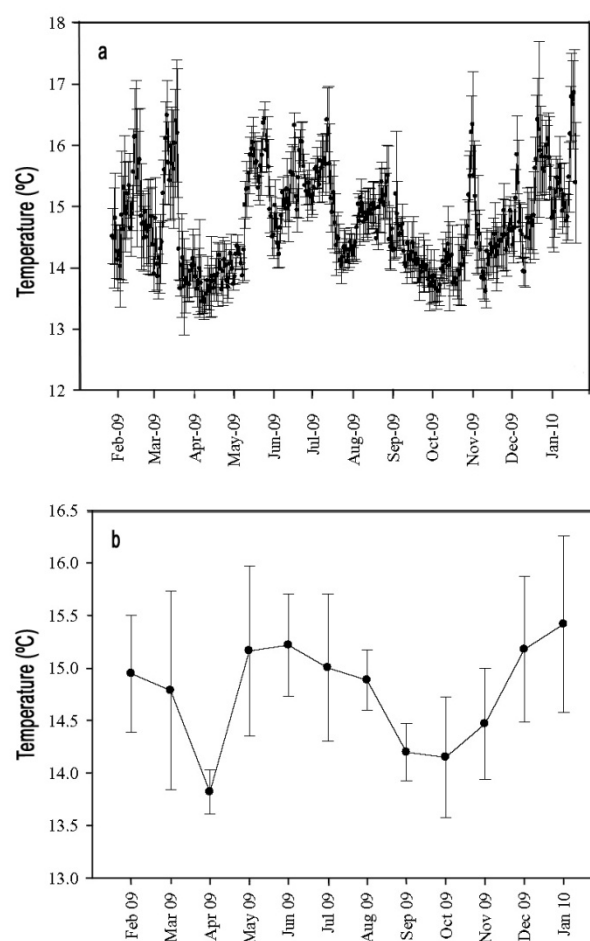


Figure 1. a) Average daily temperature variation (\pm SD), and b) average monthly temperature variation (\pm SD) registered in Chanavaya at 16 m depth between February 2009 and January 2010.

respectively, and in December–January with 85.7 and 100% respectively.

The studies carried out searching for reproductive aggregations of *T. chocolata* with specimens in copulation and clutch laying in capsules, showed their presence in 4 and 16 m depth isobaths, from early February to late August 2009, and reappearing in January 2010. The aggregations detected between early February and April were small, with no more than 100 specimens (Fig. 4a), and were located between 7 and 16 m depth. In May, only one aggregation with over 100 specimens was found at 4 m depth, while in early June new aggregations began to form at 12 m depth. In July the magnitude of these aggregations grew significantly, reaching the 14 m depth isobaths and containing several thousands of specimens (Fig. 4b). These were however extracted by the local fishers, who reported a catch of around 12

Table 1. Morisita Index (Id) and Standardized Morisita Index (Ip) obtained for *T. chocolata* between 5 to 20 m depth, February 2009 and January 2010 in the Chanavaya area.

Date	Ip	Id	Decision
Feb-2009	0.5038752	1.4621849	Aggregate
Mar-2009	-0.428408	1.2561576	Uniform
Apr-2009	0.5101076	1.5158371	Aggregate
May-2009	0.5094268	1.3852814	Aggregate
Jun-2009	0.5158942	1.5623762	Aggregate
Jul-2009	0.5061920	1.2884615	Aggregate
Aug-2009	0.5122447	1.4727664	Aggregate
Sep-2009	0.5125252	1.5918367	Aggregate
Oct-2009	0.5134572	1.5452716	Aggregate
Nov-2009	0.5220768	1.7910448	Aggregate
Dec-2009	0.5182662	1.6574074	Aggregate
Jan-2010	0.5246332	1.7819048	Aggregate

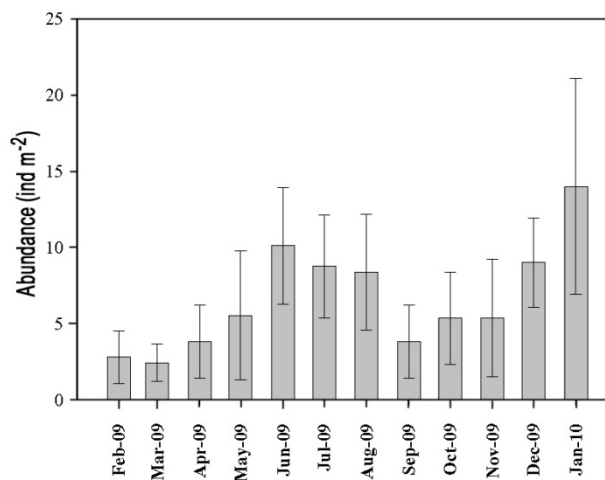


Figure 2. Monthly variation of *T. chocolata* abundance (mean \pm SD) registered in Chanavaya between 5 to 17 m depth, February 2009 and January 2010.

ton. In August, large extensions of clutches were observed in different maturity stages with the isolated presence of breeders. During October only capsules with eggs and without breeders are observed at 15 m depth. However, in January 2010, new important aggregations were registered at 5, 8, and 15 m depth, again extracted by the local fishermen.

The extractions affecting the July aggregations left clutches with unprotected eggs (Fig. 4c) causing a strong predation (Fig. 4d) by other gastropods such as *Priene* spp., *Mitrella unifasciata* (Sowerby, 1832), and *Mitra orientalis* (Griffith & Pidgeon, 1834); equinoderms such as *Stichaster striatus* (Müller & Troschel, 1840), and fishes such as *Chromis crasma*

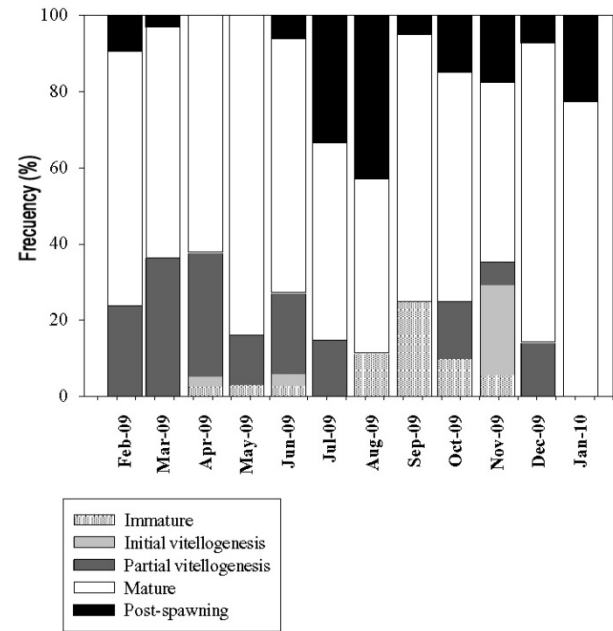


Figure 3. Monthly variation of the percentage of female *T. chocolata* specimens according to gonad maturity stages between February 2009 and January 2010.

(Valenciennes, 1833) and *Cheilodactylus variegatus* (Valenciennes, 1833).

DISCUSSION

Results obtained from the histological analysis, showed that the gonad development of *T. chocolata* is not a synchronic process, with the presence of specimens in different phases of gametogenesis development, and with predominance of mature females during the entire year. The presence of mature specimens of this resource during different months has also been mentioned in other studies (Rojas *et al.*, 1986; Andrade *et al.*, 1997; Avendaño *et al.*, 1997), as well as with other species of the same family, reported by Rojas *et al.* (1986), such as *Morula marginalba* (Blainville, 1832), *Thais emarginata* (Deshayes, 1839) and *Thais canaliculata* (Gray, 1839). An asynchronic reproductive process with significant maturity periods during some months has also been found for the Muricidae *Concholepas concholepas* (Bruguère, 1789) by Avilés & Lozada (1975) and Ramorino (1975).

The permanent existence of mature and evacuated females in variable proportions and the presence of reproductive aggregations in shallow waters, in which mainly adult specimens concentrate in high densities

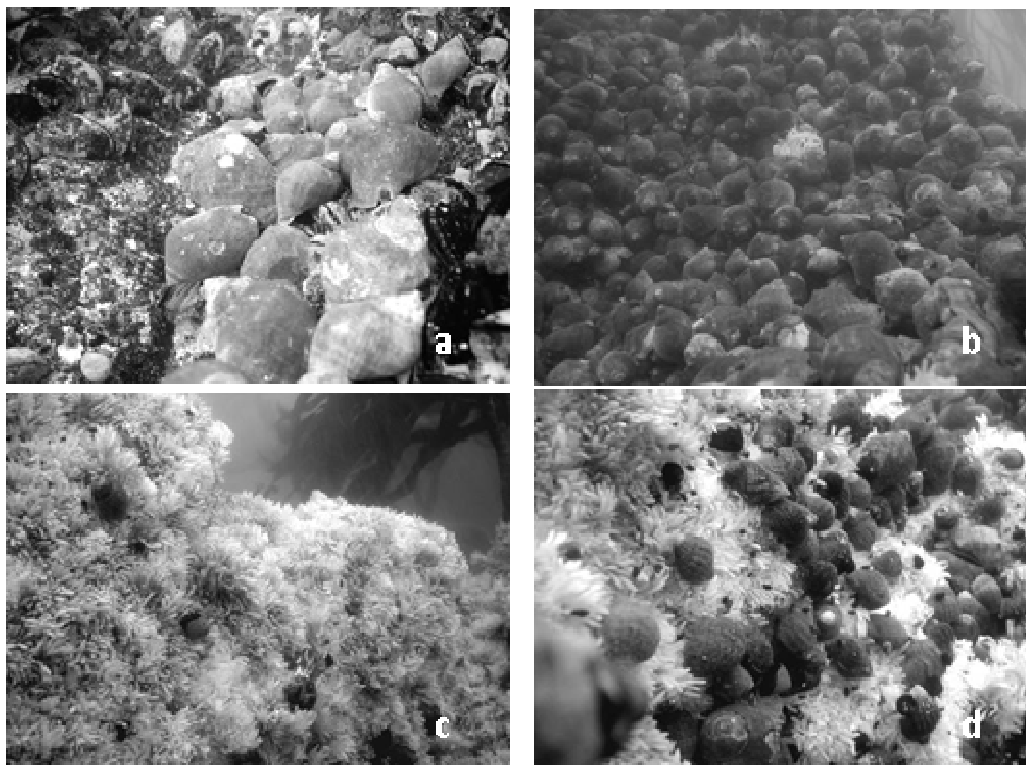


Figure 4. Aspects of *T. chocolata* reproductive aggregations. a) Small aggregations, b) large aggregations occurring during June-August, c) unprotected clutches following the extraction of breeders, d) clutch predation by other gastropods.

for copulation and clutch laying, allow us to determine that the reproductive process of *T. chocolata*, in the shallow stratus, occurs with greater or lesser intensity during the entire year. However, the increase in aggregated specimens during June-July and January, as well as the high percentage of evacuated specimens during those months, allow establishing those periods as the ones with highest reproductive activity. Intense clutch laying periods occurring during June-September and February-March have also been found for other populations in Peninsula Serrano Tarapacá (Retamales & González, 1982), while in La Rinconada (Antofagasta, Chile), large aggregations have been registered in June (Avendaño *et al.*, 1997), and in the last years, also during December-January (Cantillánez *et al.*, 2011), showing variability in the more important events. Rojas *et al.* (1986), also pointed out this variability for populations in the Pisco area in Peru, with the occurrence of intense reproduction periods in October 1974 and in August 1975. These variations in *T. chocolata* reproductive events in the northern Chile populations could be a response strategy to the temperature variability presented by the environment. In several gastropods such as *Haliotis discus hannai* (Reeve, 1846), *H. tuberculata*

(Linnaeus, 1758), *H. midae* (Linnaeus, 1758), *C. concholepas*, and *Strombus luhuanus* (Linnaeus, 1758), temperature variations have been mentioned as one of the main factors that influence gonad maturation (Peña, 1987). One of the characteristics of the studied zone is the temperature variations which alter the seasonal cycle as a response to irregular cold water upwelling processes present during most of the year, with intense periods during summer and winter (Escribano *et al.*, 1995, 2002; Blanco *et al.*, 2001). The variability of this annual cycle could explain the interannual temporal variations presented by the reproductive aggregations, which along with demonstrating the ineffectiveness of proposing fixed extraction periods could induce new studies to contrast said hypothesis.

The results obtained show that the most important reproductive aggregations (June-July and January), coincide with periods presenting temperatures above 15°C, and that the decrease in reproductive activity observed during early April is associated with a decrease in temperature maintained until early May. This relation also allowed observing that periods of abrupt temperature variations in short periods of time (decrease from 16.5 to 14.5°C between May 25 and

31; and decrease from 16.1 to 14.8°C between December 29 and 31, 2009) preceding the formation of aggregations could act as a precursor mechanism for mature specimens to begin aggregating. In the gastropod (Muricidae) *Plicopurpura pansa* (Gould, 1853) reproduction begins following a temperature drop (Michel-Morfin *et al.*, 2002).

Although the results show an aggregate distribution of *T. chocolata* during the entire year, the abundance of specimens found within the stratum containing reproductive aggregations (5 to 17 m) increased before, during and following the formation of these aggregations. This shows a change in the degree of spatial aggregation in these periods, as has been observed in the La Rinconada population (Avendaño *et al.*, 2010). This increase in population density in the shallow levels, independent of the formation of aggregations, could be used as an indicator of the reproductive activity of *T. chocolata* for monitoring future aggregation and clutch laying processes.

The specimen's strategy of aggregating in shallow waters to reproduce could guarantee the dispersion of the larvae, considering that *T. chocolata* presents planktotrophic teleplanic larvae, which after remaining approximately one month in the capsules and four months in plankton reaches competition (Romero *et al.*, 2004). Long larval life periods extending over several months in larvae capable of responding positively to light and establishing close to the surface, as occurs with the larvae of several gastropods, reflects their capacity of overcoming major biogeographic barriers for colonization after being dispersed by wind and surface currents (Scheltema, 1989; Gasca *et al.*, 1994; Stoner & Smith, 1998; Oliva-Rivera & De Jesús-Navarrete, 2000). The *in situ* observations carried out show that the aggregations in shallow waters also provide protection to the clutch capsules until the hatching and dispersal of the larvae, with the adult breeders avoiding predation with their bodies. This has also been indicated for the gastropods *Fusitriton oregonensis* (Redfield, 1846), *Thais lamellosa* (Gmelin, 1791), and *Purpura pansa* (Gould, 1853) (Stickle & Mrozek, 1973; Acevedo & Hernández, 1988).

The combined effect generated by the extraction of aggregated specimens, the predation on the clutches following this extraction and the long larval life cycle greatly increase vulnerability levels and would be the main causes for uncertainty concerning the extraction process which has unbalanced the ecosystem dynamics where the species develops. This calls for a greater protection of the resource during the reproductive aggregation process, which has been

shown to vary in time making the establishment of closed seasons an ineffective means to manage this objective.

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