

DEPARTMENT OF COMMERCE

National Oceanic and Atmospheric Administration

50 CFR Parts 223 and 224

[Docket No. 240626–0177; RTID 0648– XF174]

Endangered and Threatened Wildlife and Plants; Proposed Listing Determinations for Ten Species of Giant Clams Under the Endangered Species Act

AGENCY: National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA), Commerce.

ACTION: Proposed rule; availability of status review; request for comments.

SUMMARY: We, NMFS, have completed a comprehensive status review of seven species of giant clams (*Hippopus hippopus, H. porcellanus, Tridacna derasa, T. gigas, T. mbalavuana, T. squamosa,* and *T. squamosina*) in response to a petition to list these species as threatened or endangered under the Endangered Species Act (ESA). Based on the best scientific and commercial data available, including the Status Review Report, and after taking into account efforts being made to protect these species, we have determined that *H. porcellanus, T. mbalavuana,* and *T. squamosina* are in danger of extinction throughout the entirety of their respective ranges, *T. derasa* and *T. gigas* are in danger of extinction in a significant portion of their respective ranges, and *H. hippopus* is likely to become an endangered species within the foreseeable future throughout a significant portion of its range. Therefore, we propose to list *H. porcellanus, T. mbalavuana, T. squamosina, T. derasa,* and *T. gigas* as endangered species and *H. hippopus* as a threatened species under the ESA. We have determined that the fluted clam, *T. squamosa,* is not currently in danger of extinction throughout all or a significant portion of its range and is not likely to become so within the foreseeable future. Therefore, we find that *T. squamosa* does not meet the definition of a threatened or an endangered species under section 4(a) of the ESA. Further, we propose to exercise the discretionary authority of section 4(d) to extend the prohibitions of section 9 of the ESA to the proposed threatened species, *H. hippopus.* At this time, we do not propose to designate critical habitat for the three species proposed to be listed that occur within U.S. jurisdiction (*H. hippopus, T. derasa,* and *T. gigas*)

because critical habitat for these species is not yet determinable. Using the authority of section 4(e) of the ESA, we also propose to list *T. crocea, T. maxima, T. noae,* and *T. squamosa* as threatened species due to the similarity of appearance of products derived from these species (*e.g.,* meat, worked shell products, and pearls) to those derived from the six aforementioned species proposed to be listed based on their extinction risk. We propose a special rule to define activities that would and would not be prohibited with respect to these four species in order to mitigate the substantial enforcement challenge associated with this similarity of appearance concern. We solicit information to inform the final listing determination and to inform a future proposal for any determinable critical habitat.

DATES: Comments must be received by October 23, 2024.

Public informational meetings and public hearings: In-person and virtual public hearings on this proposed rule will be held during the public comment period at dates, times, and locations to be announced in a forthcoming **Federal Register** notice.

ADDRESSES: You may submit data, information, or written comments on this document, identified by NOAA– NMFS–2017–0029, by either of the following methods:

• *Electronic Submissions:* Submit all electronic public comments via the Federal e-Rulemaking Portal. Go to *<https://www.regulations.gov>* and enter *NOAA–NMFS–2017–0029* in the Search box. Click on the ''Comment'' icon, complete the required fields, and enter or attach your comments.

• *Mail:* Submit written comments to Endangered Species Division, Office of Protected Resources (F/PR3), National Marine Fisheries Service, 1315 East West Highway, Silver Spring, MD 20910, USA, Attn: Giant Clams Species Listing Proposed Rule.

Instructions: Comments sent by any other method, to any other address or individual, or received after the end of the comment period, may not be considered by NMFS. All comments received are a part of the public record and will generally be posted for public viewing on *<https://www.regulations.gov>* without change. All personally identifying information (*e.g.,* name, address, *etc.*), confidential business information, or otherwise sensitive information submitted voluntarily by the sender will be publicly accessible. NMFS will accept anonymous comments (enter ''N/A'' in the required

fields if you wish to remain anonymous).

The Status Review Report associated with this determination, its references, and the petition can be accessed electronically at: *[https://](https://www.fisheries.noaa.gov/action/proposed-rule-10-species-giant-clams-under-endangered-species-act) [www.fisheries.noaa.gov/action/](https://www.fisheries.noaa.gov/action/proposed-rule-10-species-giant-clams-under-endangered-species-act) [proposed-rule-10-species-giant-clams](https://www.fisheries.noaa.gov/action/proposed-rule-10-species-giant-clams-under-endangered-species-act)[under-endangered-species-act.](https://www.fisheries.noaa.gov/action/proposed-rule-10-species-giant-clams-under-endangered-species-act)* The peer review plan, associated charge statement, and peer review report can be accessed electronically at: *[https://](https://www.noaa.gov/information-technology/status-review-report-of-7-giant-clam-species-petitioned-under-us-endangered-species-act-hippopus) [www.noaa.gov/information-technology/](https://www.noaa.gov/information-technology/status-review-report-of-7-giant-clam-species-petitioned-under-us-endangered-species-act-hippopus) status-review-report-of-7-giant-clamspecies-petitioned-under-us[endangered-species-act-hippopus.](https://www.noaa.gov/information-technology/status-review-report-of-7-giant-clam-species-petitioned-under-us-endangered-species-act-hippopus)* The draft Environmental Assessment and Initial Regulatory Flexibility Analysis associated with the proposed ESA section 4(d) regulation for *T. crocea, T. maxima, T. noae,* and *T. squamosa* can be accessed electronically via the Federal e-Rulemaking Portal by navigating to *[https://](https://www.regulations.gov) www.regulations.gov* and entering *NOAA–NMFS–2017–0029* in the Search box.

FOR FURTHER INFORMATION CONTACT: John Rippe, NMFS Office of Protected Resources, (301) 427–8467, *[john.rippe@](mailto:john.rippe@noaa.gov) [noaa.gov.](mailto:john.rippe@noaa.gov)*

SUPPLEMENTARY INFORMATION:

Background

On August 7, 2016, we received a petition from Dwayne Meadows to list 10 species of giant clams (Cardiidae: Tridacninae) as threatened or endangered under the ESA throughout their respective ranges. The petitioner also requested that critical habitat be designated in waters subject to U.S. jurisdiction concurrently with listing under the ESA. On June 26, 2017, we published a 90-day finding (82 FR 28946) announcing that the petition presented substantial scientific or commercial information indicating that the petitioned action may be warranted for 7 of the 10 species listed in the petition: *Hippopus hippopus* (horse's hoof, bear paw, or strawberry clam), *Hippopus porcellanus* (porcelain or China clam), *Tridacna derasa* (smooth giant clam), *Tridacna gigas* (true giant clam), *Tridacna mbalavuana* (syn. *T. tevoroa;* devil or tevoro clam), *Tridacna squamosa* (fluted or scaly clam), and *Tridacna squamosina* (syn. *T. costata;* Red Sea giant clam), but that the petition did not present substantial scientific or commercial information indicating that the petitioned action may be warranted for the other 3 species (*T. crocea, T. maxima,* or *T. noae*). We also announced the initiation of a status review of the seven aforementioned giant clam species, as required by

section 4(b)(3)(A) of the ESA, and requested information to inform the agency's decision on whether these species warrant listing as endangered or threatened under the ESA. We received information from the public in response to the 90-day finding and incorporated the information into both the Status Review Report (Rippe *et al.,* 2023) and this proposed rule. This information complemented our thorough review of the best available scientific and commercial data for these species (see *Status Review* below).

Listing Determinations Under the Endangered Species Act

We are responsible for determining whether species are threatened or endangered under the ESA (16 U.S.C. 1531 *et seq.*). To be considered for listing under the ESA, a group of organisms must constitute a ''species,'' which is defined in section 3 of the ESA to include any subspecies of fish or wildlife or plants, and any distinct population segment (DPS) of any species of vertebrate fish or wildlife which interbreeds when mature (16 U.S.C. 1532(16)). On February 7, 1996, NMFS and the U.S. Fish and Wildlife Service (USFWS; together, the Services) adopted a policy describing what constitutes a DPS of a taxonomic species (''DPS Policy,'' 61 FR 4722). The joint DPS Policy identifies two elements that must be considered when identifying a DPS: (1) The discreteness of the population segment in relation to the remainder of the taxon to which it belongs; and (2) the significance of the population segment to the remainder of the taxon to which it belongs. Because giant clams are invertebrates they cannot be listed as DPSs, and the DPS Policy does not apply here.

Section 3 of the ESA defines an endangered species as ''any species which is in danger of extinction throughout all or a significant portion of its range'' and a threatened species as one ''which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.'' Thus, we interpret an ''endangered species'' to be one that is presently in danger of extinction. A ''threatened species,'' on the other hand, is not presently in danger of extinction, but is likely to become so within the foreseeable future (that is, at a later time). In other words, the primary statutory difference between a threatened and endangered species is the timing of when a species is in danger of extinction, either presently (endangered) or in the foreseeable future (threatened).

Under section 4(a)(1) of the ESA, we must determine whether any species is endangered or threatened as a result of any one or a combination of any of the following factors: (A) the present or threatened destruction, modification, or curtailment of its habitat or range; (B) overutilization for commercial, recreational, scientific, or educational purposes; (C) disease or predation; (D) the inadequacy of existing regulatory mechanisms; or (E) other natural or manmade factors affecting its continued existence (16 U.S.C. 1533(a)(1)); 50 CFR 424.11(c). We are also required to make listing determinations based solely on the best scientific and commercial data available, after conducting a review of the species' status and after taking into account efforts, if any, being made by any State or foreign nation (or subdivision thereof) to protect the species (16 U.S.C. 1533(b)(1)(A)).

On July 5, 2022, the U.S. District Court for the Northern District of California issued an order vacating the ESA section 4 implementing regulations that were revised or added to 50 CFR part 424 in 2019 (''2019 regulations,'' see 84 FR 45020, August 27, 2019) without making a finding on the merits. On September 21, 2022, the U.S. Court of Appeals for the Ninth Circuit granted a temporary stay of the district court's July 5 order. On November 14, 2022, the Northern District of California issued an order granting the government's request for voluntary remand without vacating the 2019 regulations. On April 5, 2024, the Services published a final rule revising the section 4 implementing regulations (89 FR 24300). Because the 2024 revised regulations became effective on May 6, 2024, we considered them during the development of this proposed rule. For purposes of this determination and in an abundance of caution, we considered whether the analysis or its conclusions would be any different under the pre-2019 regulations. We have determined that our analysis and conclusions presented here would not be any different.

Status Review

To determine whether each of the seven giant clam species warrants listing under the ESA, we completed a Status Review Report, which summarizes information on each species' taxonomy, distribution, abundance, life history, and biology; identifies threats or stressors affecting the status of each species; and assesses the species' current and future extinction risk. We appointed a biologist in the Office of Protected Resources Endangered Species Conservation Division to compile and complete a

scientific review of the best scientific and commercial data available on the giant clam species, including information received in response to our request for information (82 FR 28946, June 26, 2017).

The Status Review Report was subject to independent peer review pursuant to the Office of Management and Budget Final Information Quality Bulletin for Peer Review (M–05–03; December 16, 2004). It was peer reviewed by four independent specialists selected from the academic and scientific community with expertise in giant clam biology, conservation, and management. The peer reviewers were asked to evaluate the adequacy, appropriateness, and application of data used in the Status Review Report, as well as the findings made in the ''Assessment of Extinction Risk'' section of the report. All peer reviewer comments were addressed prior to finalizing the Status Review Report and publication of this finding.

We subsequently reviewed the Status Review Report, its cited references, and peer review comments, and conclude that it synthesizes the best available scientific and commercial data related to the seven giant clam species considered here. In making our determinations, we have applied the statutory provisions of the ESA, our regulations regarding listing determinations, and relevant policies identified herein.

The Status Review Report and the peer review report are available on our website (see **ADDRESSES** section). Below is a summary of the information from the Status Review Report and our analysis of the status of the seven giant clam species.

Biological Review

Taxonomy and Species Descriptions

Giant clams are a small but conspicuous group of the planet's largest and fastest growing marine bivalves. They fall within the order Veneroida, family Cardiidae, and subfamily Tridacninae (Schneider, 1998). For many years, giant clams were considered to occupy their own family (Tridacnidae) sister to Cardiidae until molecular phylogenetics (Maruyama *et al.,* 1998; Schneider & Foighil, 1999) and comparison of sperm ultrastructure (Keys & Healy, 2000) supported reclassifying the group as a subfamily within Cardiidae. This is the current, most widely accepted classification; however, Neo *et al.* (2017) note that others continue to argue that Tridacnidae should be retained as a full family based on its highly distinct

morphology (Huber & Eschner, 2011; Penny & Willan, 2014).

Colloquially described as having 'upside down' orientation (Penny & Willan, 2014), giant clams lie with the hinge of their shell facing downwards, allowing their byssus (*i.e.,* filamentous threads) to attach the organism to the substrate while orienting their enlarged mantle upwards toward the sunlight (Soo & Todd, 2014). Additionally, most giant clam species have an epifaunal lifestyle (*i.e.,* situated on top of the substrate) in contrast to the largely infaunal lifestyle of their cardiid ancestors.

There are two extant genera of giant clams, *Hippopus* and *Tridacna,* which are distinguished by several shell and mantle characteristics. In *Hippopus,* a very narrow byssal orifice is bordered by interlocking teeth, while *Tridacna* exhibits a well-defined byssal gape without teeth. Additionally, when the clam is completely open, the mantle of *Tridacna* extends laterally beyond the margin of the shell, whereas the mantle of *Hippopus* does not (Lucas, 1988). A result of this difference is that *Hippopus* species tend to gape their valves further apart than *Tridacna* species, thus exposing more mantle surface area (Lucas, 1994).

There are currently 12 species of giant clams recognized in the literature, though this number changes often as advances in molecular phylogenetics resolve evolutionary relationships (including cryptic speciation) that had been overlooked by traditional morphology-based taxonomies. Joseph Rosewater's seminal work in 1965 is widely cited as the authoritative material for early descriptions of giant clam species and includes six current species that remain valid to date: *H. hippopus* (Linnaeus, 1758), *T. gigas* (Linnaeus, 1758), T. derasa (Röding, 1798), *T. maxima* (Röding, 1798), *T. squamosa* (Lamarck, 1819), and *T. crocea* (Lamarck, 1819). He later added *H. porcellanus* to this list after reexamining its classification (Rosewater, 1982).

At the time of the 1965 report, *T. mbalavuana* had only been formally described from fossils on Viti Levu, Fiji. However, Fijians had long known of this species occurring in local waters as 'tevoro', or devil clam. Thus, when Lucas *et al.* (1991) re-discovered the species in 1991, they described it as the new species *T. tevoroa.* It was not until 2000 that *T. mbalavuana* and *T. tevoroa* were re-classified as synonymous based on morphological similarities (Newman & Gomez, 2000). As in the Status Review Report, we refer to this species by its lectotype (*i.e.,* its original

classification), *T. mbalavuana.* Additionally, Richter *et al.* (2008) described a new species, *T. costata,* in 2008, but upon further analysis, it too was found to be synonymous with a previously described species, *T. squamosina,* first discovered by Rudolf Sturany (1899) during the early Austro-Hungarian expeditions of the Red Sea (Huber & Eschner, 2011). As in the Status Review Report, we refer to this species by its lectotype, *T. squamosina.*

Based on the best available scientific and commercial data summarized above, we find that all seven species of giant clams (*H. hippopus, H. porcellanus, T. derasa, T. gigas, T. mbalavuana, T. squamosa,* and *T. squamosina*) are currently considered taxonomically-distinct species and, therefore, meet the definition of ''species'' pursuant to section 3 of the ESA. Distinguishing features of each species are summarized below.

Hippopus Hippopus

Commonly referred to as the horse's hoof, bear paw, or strawberry clam, *H. hippopus* has a heavy, thick shell that features prominent reddish blotches in irregular concentric bands (Rosewater, 1965). The shell interior is porcellaneous white, frequently flushed with yellowish orange on the ventral margin (Kinch & Teitelbaum 2010; Rosewater, 1965). Primary radial sculpture consists of 13 or 14 moderately convex rib-like folds over the surface of the valve, extending towards the ventral slope where they become obsolete (Rosewater, 1965). The mantle usually exhibits mottled patterns in green, yellow-brown or grey, and the incurrent siphon lacks guard tentacles (Neo *et al.,* 2017). Juveniles and young, smaller adults are usually attached to coral rubble by their byssus, whereas older (larger, heavier) individuals are typically found unattached on the substratum being held in place by their weight (Rosewater, 1965; Neo *et al.,* 2017). The largest reported shell length for *H. hippopus* is 50 cm, which was documented at the Bolinao Marine Laboratory in the Philippines (Neo *et al.,* 2017).

Hippopus Porcellanus

Commonly referred to as the China clam, *H. porcellanus* grows to a maximum size of 40 cm, but is most commonly found at shell lengths of around 20 cm (Kinch & Teitelbaum, 2010). The shell exterior is off-white, occasionally with scattered weak reddish blotches. The shell interior is porcellaneous white, often flushed with orange on the ventral margin, and the mantle ranges from a yellowish-brown

to a dull green or grey (Kinch & Teitelbaum, 2010). This species is distinguished from its congener, *H. hippopus,* by its smoother and thinner valves and presence of fringing tentacles at the incurrent siphon (Neo, Eckman, *et al.,* 2015).

Tridacna Derasa

T. derasa, or the smooth giant clam, is the second largest giant clam species, with a maximum size of around 60 cm (Neo *et al.,* 2017). *T. derasa* has a heavy, plain-colored shell and can be distinguished from other species by its low primary and secondary radial sculpture. Primary radial sculpture consists of 7–12 broad, shallow rib-like folds (usually 6–7 main folds), and the shells are often greatly thickened at the umbos (*i.e.,* the oldest, most prominent point of the shell near the ventral margin) (Rosewater, 1965). The mantle is often characterized by elongate patterns of brilliant greens and blues, and the incurrent siphon is equipped with inconspicuous guard tentacles (Neo *et al.,* 2017).

Tridacna Gigas

T. gigas is known as the true giant clam and is the largest of all the giant clam species, growing to a maximum shell length of 137 cm and maximum weight in excess of 225 kg (Beckvar, 1981; Rosewater, 1965). The shell of *T. gigas* is thick and heavy, equivalve (having valves of the same size), and equilateral (symmetrical front-to-back) (Hernawan, 2012). The shell exterior is off-white, and is often covered with marine growths (*e.g.,* vermetids, annelid tubes, coral, *etc.*) (Kinch & Teitelbaum, 2010; Rosewater, 1965). For the most part, the shell lacks scales except near the byssal orifice where small scales may be present. The shell interior is porcellaneous white, dull in the area within the pallial line, and shiny above the pallial line to the dorsal end of the shell (Rosewater, 1965). Often, the mantle is yellowish-brown to olivegreen and is a darker shade along the mantle's edge and around the clam's siphons (Rosewater, 1965). Numerous, small, brilliant blue-green rings are dispersed across the mantle, each enclosing one or several hyaline organs. These rings are especially prevalent along the lateral edges of the mantle and around the siphonal openings (Rosewater, 1965). Smaller specimens (*i.e.,* 150–200 mm) may be more uniformly colored, lacking a darker shade along the edge of the mantle and with fewer colored rings (Rosewater, 1965).

T. gigas is readily identified by many characteristics, most notably its large

size. The species can also be identified by four to six unique deep radial folds that give way to elongate, triangular projections at the upper margins of its shells (Hernawan, 2012; Lucas, 1988), a complete outer demibranch (the Vshaped structure of gills common to bivalves; Rosewater, 1965), the lack of tentacles on the inhalant siphon (Hernawan, 2012), and the lack of byssal attachment (*i.e.,* they are free-living; Rosewater, 1965).

Tridacna Mbalavuana

Before it was formally classified taxonomically, Fijians had long referred to *T. mbalavuana* as 'tevoro,' or devil clam, based on its thin, sharply-edged valves and warty brownish grey mantle. *T. mbalavuana* has been hypothesized to be a transitional species between the *Hippopus* and *Tridacna* genera due to overlapping characteristics (Lucas *et al.,* 1991; Schneider & Foighil, 1999). It has *Hippopus*-like features including the absence of a byssal gape, a mantle that does not extend over the shells, and the absence of hyaline organs (Lucas *et al.,* 1991); however, *T. mbalavuana* looks most like *T. derasa* in appearance (Lewis & Ledua, 1988). It can be distinguished from *T. derasa* by its rugose mantle, prominent guard tentacles on the incurrent siphon, thinner valves, and colored patches on the shell ribbing (Neo, Eckman, *et al.,* 2015). The shell exterior is off-white, often partly encrusted with marine growths. It can grow to just over 50 cm long (Lewis & Ledua, 1988; Neo, Eckman, *et al.,* 2015) with the largest specimen recorded at 56 cm (Lucas *et al.,* 1991).

Tridacna Squamosa

Commonly known as the fluted or scaly giant clam due to the characteristic leaf-like projections on its valves, *T. squamosa* is one of the most widely distributed species of giant clams. The exterior of its shell is greyish white in color, often with various hues of orange, yellow, or pink/mauve (Rosewater, 1965). The primary radial sculpture consists of 4–12 strongly convex, rib-like folds. The concentric sculpture consists of ''undulate lines of growth which produce widely spaced, broadly leaf-like, projecting scales on primary folds'' (Rosewater, 1965). The prominent scales on the shell commonly feature different shades or colors (Kinch & Teitelbaum, 2010). The shell interior is porcellaneous white, with an occasional hint of orange (Kinch & Teitelbaum, 2010). Rosewater (1965) describes the mantle as having a main ground color of greyish purple with a row of light blue rhomboidal spots along

the outer mantle margin and multicolored irregularly-circular spots toward the center. The outer periphery of the spots is pale yellow, inside of which is a band of dark yellow, and the entire center is nearest to light blue. Generally, *T. squamosa* reaches a maximum shell length of ∼40 cm (Neo *et al.,* 2017).

Tridacna Squamosina

T. squamosina, or the Red Sea giant clam, exhibits a strong resemblance to *T. squamosa,* but can be distinguished by its asymmetrical shells, crowded scutes, wider byssal orifice, and five to seven deep triangular radial folds (Roa-Quiaoit, 2005; Richter *et al.,* 2008). Additionally, the mantle is most commonly a subdued brown mottled pattern with a green margin that features prominent ''wart-like'' protrusions and pale markings following the mantle contour (Richter *et al.,* 2008). These are the main diagnostic features separating *T. squamosina* from its sympatric congeners and are conservatively present even in small clams <10 cm shell length (Richter *et al.,* 2008). *T. squamosina* can reach at least 32 cm in shell length (Neo, Eckman, *et al.,* 2015)—the largest specimen recorded was found in the southern Red Sea at Kamaran Island, off the coast of Yemen (Huber & Eschner, 2011).

Range, Distribution, and Habitat Use

H. Hippopus

H. hippopus is widely distributed throughout the Indo-Pacific (*i.e.,* the tropical and subtropical waters of the Indian Ocean, the western and central Pacific Ocean, and the seas connecting the two in the general area of Indonesia), occurring from the Andaman and Nicobar Islands in the west to the Republic of Kiribati in the east, and from New Caledonia in the south to the southern islands of Japan in the north (Neo *et al.,* 2017).

According to Munro (1993a), *H. hippopus* occurs in the widest range of habitat types of all the giant clam species. Most often, it is found in shallow, nearshore patches of reef, sandy areas and seagrass beds that can be exposed during low tides, but it can also be found on reefs as deep as 10 m (S. Andréfouët, pers. obs. cited in Neo *et al.,* 2017). Based on a recent survey in New Caledonia, Purcell *et al.* (2020) found that *H. hippopus* ''strongly preferred'' lagoonal reefs. The authors hypothesized that the species may either prefer the siltier sediments and more turbid water of lagoon reef flats or alternatively may have low tolerance to the wave exposure of barrier reefs.

H. Porcellanus

H. porcellanus has one of the most restricted geographic ranges of the giant clams, centered in the Coral Triangle region. The species is mostly known from the Sulu Archipelago and Palawan region in the Philippines, but it has also been reported in Palau, the Milne Bay Province (Papua New Guinea), Sabah (Malaysia), and Sulawesi and Raja Ampat (Indonesia) (S. Wells, 1997; Neo *et al.,* 2017).

There is very little information specifying the habitat preferences of *H. porcellanus,* but according to Calumpong (1992), the species is commonly found in shallow, nearshore sandy areas adjoining coral reefs. Juvenile or young *H. porcellanus* are frequently found byssally attached to coral heads, whereas larger mature *H. porcellanus* can be found on sandy bottoms unattached to substrate (Rosewater, 1982; Kinch & Teitelbaum, 2010).

T. Derasa

The geographic range of *T. derasa* primarily encompasses the Coral Triangle region, although it extends east to Tonga and as far west as the Cocos (Keeling) Islands in the eastern Indian Ocean (Rosewater, 1965). Adams *et al.* (1988) described *T. derasa* as having a patchy distribution, being rare in many places throughout its range and abundant in others. Notably, *T. derasa* has been one of the most widely cultured species of giant clam and has been introduced to a number of countries and territories throughout the central and western Pacific Ocean. This includes the Federated States of Micronesia (FSM), Marshall Islands, Tuvalu, Cook Islands, Samoa, and American Samoa.

T. derasa preferentially inhabits clear offshore waters distant from areas of significant freshwater run-off (Munro, 1993a). According to Calumpong (1992), the species appears to favor oceanic environments (*i.e.,* small islands and atolls) more than fringing reefs adjacent to large island masses. The species is known to occur at depths of 4–25 m (Lewis *et al.,* 1988; Neo *et al.,* 2017), and is usually found weakly attached to the tops and sides of coral outcrops as juveniles, but may become detached upon reaching a larger size (Adams, 1988).

T. Gigas

The natural range of *T. gigas* spans the shallow waters of the Indo-Pacific and the Great Barrier Reef, from Myanmar in the west to the Republic of Kiribati in the east, and from the Ryukyus Islands

of southern Japan in the north to Queensland, Australia in the south (bin Othman *et al.,* 2010; Neo *et al.,* 2017). Cultured specimens of *T. gigas* have been introduced in American Samoa, the Cook Islands, Hawaii, and Samoa (Neo *et al.,* 2017). Like most other giant clam species, *T. gigas* is typically associated with coral reefs and can be found in many habitats, including highand low-islands, atoll lagoons, and fringing reefs (Munro, 1993a). In a broad survey of *T. gigas* distribution throughout the Great Barrier Reef, Braley (1987a) found that the species was most common on inshore reefs potentially influenced by seasonal fluctuations in salinity and turbidity and was rare south of 19° S. The observed distribution was essentially opposite of that for *T. derasa,* which was found primarily on offshore reefs and was common in the Swain Reefs at 21–22° S. These contrasting distributions led Braley (1987b) to the conclusion that temperature may limit the distribution of young *T. gigas,* while *T. derasa* may be more sensitive to salinity and/or turbidity. *T. gigas* is typically found between the depths of 2 to 20 m and is often found among *Acropora* spp. or other hard coral communities, hard reef substrata, or on bare sand (Braley, 1987b; Kinch & Teitelbaum 2010; Rosewater, 1965).

T. Mbalavuana

T. mbalavuana has one of the most restricted distributions of all the giant clam species. For many years, it had only been observed in Fiji and Tonga, but recent reports indicate that this species may be found in low numbers outside of these two locations. According to Kinch and Teitelbaum (2010), *T. mbalavuana* had been observed in the Loyalty Islands in New Caledonia, a report later supported by Tiavouane and Fauvelot (2016), who encountered two individuals on the northeastern barrier reef of New Caledonia after ''exhaustive searches'' (Neo *et al.,* 2017). Single individuals were also reportedly observed on Lihou Reef in the Coral Sea (Ceccarelli *et al.,* 2009) and in the Raja Ampat region of West Papua, Indonesia (Wakum *et al.,* 2017), but neither of these reports have been further corroborated.

In Fiji, individuals are most often observed along outer slopes of leeward reefs in the eastern Lau Islands, in very clear, oceanic water (Ledua *et al.,* 1993). In Tonga, they are found in the northern Vava'u and Ha'apai islands. *T. mbalavuana* has a deeper depth distribution than most other giant clam species. In one study on spawning and larval culture of *T. mbalavuana,*

individuals were collected from waters of Fiji and Tonga (Ledua *et al.,* 1993). The mean depth of clams collected in Fiji was 27.4 m, with samples collected from depths ranging from 20 to 33 m, and all specimens were found on the leeward side of reefs and islands. Many of the clams found in Tonga were next to the edge of a sand patch and cradled against rocky outcrops, rubble or bare rock with steep slopes (Ledua *et al.,* 1993).

T. Squamosa

T. squamosa is the second-most widely distributed giant clam species, with a broad geographic range that extends from the Red Sea and eastern Africa in the west to the Pitcairn Islands in the east, and from the Great Barrier Reef in the south to southern Japan in the north (bin Othman *et al.,* 2010; Neo *et al.,* 2017). The species has also been introduced in Hawaii and Guam (CITES, 2004b).

T. squamosa is usually found on coral reefs or on adjacent sandy areas (Neo *et al.,* 2017). Juveniles are often attached to the substrate by a ''weak but copious byssus,'' while adults can be found either attached or free-living (Neo *et al.,* 2017; Rosewater, 1965). *T. squamosa* occurs across a broad depth range, which includes shallow reef flats, patch reefs, and reef slopes, both inside and outside of lagoons. Individuals have been observed as deep as 42 m in the Red Sea (Jantzen *et al.,* 2008). *T. squamosa* is typically more common on shelving fringing reefs than reef flats (Govan *et al.,* 1988) and seems to prefer sheltered environments (Kinch & Teitelbaum, 2010; Munro, 1993a). Comparing the distribution of *T. squamosa* and *T. maxima* in Mauritius, Ramah *et al.* (2017) found that *T. squamosa* were most often attached to flat substrata, such as dead plate corals or rubble. Hardy and Hardy (1969) reported that *T. squamosa* and *H. hippopus* occupied much the same habitat in Palau, both being widely distributed in relatively shallow water in the lagoon and on the barrier and fringing reefs; although, *T. squamosa* was reportedly more commonly associated with coral areas of *Acropora* spp. than adjacent sandy areas. In New Caledonia, Purcell *et al.* (2020) interpreted the relatively high abundance of *T. squamosa* on barrier reef sites compared to lagoonal reefs as indication that the species may prefer cleaner waters, as opposed to the siltier sediments and more turbid seawater of lagoon reef flats. However, Lewis *et al.* (1988) note that the species is more tolerant of turbid water than *T. derasa.* Paulay (1987) reported that all

observations of *T. squamosa* in the Cook Islands were from the outer reef slope, occasionally to depths of 30 m or more.

T. Squamosina

T. squamosina is endemic to the Red Sea, with its past and present distribution including the northeastern Gulf of Aqaba, the Sinai coast, and eastern coast of the Red Sea down to Yemen (Huber & Eschner, 2011; Lim *et al.,* 2021; Richter *et al.,* 2008; Rossbach *et al.,* 2021). There have also been several anecdotal accounts of the species in Mozambique; however, later evidence of genetic divergence between specimens in the Red Sea and Mozambique (Moreels, 2018), as well as the significant geographic distance from its central range, suggests that the reported sightings may be of its recently-resurrected sister species, *T. elongatissima,* with which it shares a close phylogenetic history (Fauvelot *et al.,* 2020; Tan *et al.,* 2021). For this reason, without more information to verify these anecdotal sightings, we do not include the Western Indian Ocean in the natural range of *T. squamosina.*

In a survey of giant clams in the Red Sea, Richter *et al.* (2008) noted that live specimens of *T. squamosina* were found exclusively in very shallow water habitats (*e.g.,* reef flats, rocky and sandy-rubble flats, seagrass beds, or under branching corals or coral heads shallower than 2m). Thus, unlike the other two Red Sea species (*T. maxima* and *T. squamosa*), which have broad depth distributions, *T. squamosina* is restricted to the reef top and is usually weakly attached to the substrate (Richter *et al.,* 2008).

Diet and Feeding

During the earliest stages of larval development, giant clams initially rely on nutrients stored in the egg yolk. Upon formation of the velum and hollow intestines within the first 2–3 days after fertilization, veliger larvae transition to planktivory and are able to actively ingest flagellates (∼5 μm in diameter), zooxanthellae and dissolved organic nutrients from the seawater via the mouth (Fitt *et al.,* 1984; Soo & Todd, 2014). Like most bivalves, giant clams retain the ability to filter feed into adulthood by pumping water into their mantle cavities via an inhalant siphon, filtering plankton through ciliated gills, and passing the filtered water back out via an excurrent siphon (Hardy & Hardy, 1969).

However, a defining characteristic of giant clams is their mutualistic relationship with dinoflagellates of the family Symbiodiniaceae, known commonly as zooxanthellae, which

provide the primary source of nutrition to adult clams. Giant clams strictly acquire symbiotic algae from the seawater during larval development and therefore do not inherit symbionts via parental oocytes (Fitt & Trench, 1981; Hartmann *et al.,* 2017). Furthermore, zooxanthellae are housed extracellularly within a diverticular extension of the digestive tract (Norton *et al.,* 1992). This 'tubular system' extends throughout the upper levels of the mantle and is arranged as a dense network of tertiary canals branching off of secondary structures with no direct connection to the haemolymph of the clam (Norton *et al.,* 1992). Detailed scanning electron microscope images have shown that zooxanthellae are often stacked in pillars within these canals and are colocated with light-scattering iridocyte cells that enhance photosynthesis (L. Rehm, unpub.) and protect the algal cells from damaging UV radiation (Rossbach, Overmans, *et al.,* 2020; Rossbach, Subedi, *et al.,* 2020).

Symbiosis is thought to be established during metamorphosis from pediveliger to the juvenile clam. At this point, zooxanthellae can be observed migrating from the stomach to the tubular system (Fitt *et al.,* 1986; Norton *et al.,* 1992). Although, more recent studies have shown that genes known to be associated with symbiosis and glycerol synthesis are expressed in giant clam larvae, suggesting that symbiotic activity may be initiated earlier during larval development (Mies *et al.,* 2016; Mies, Voolstra, *et al.,* 2017).

Giant clams receive the majority of their metabolic carbon requirements via symbiotic autotrophy. They provide dissolved inorganic nutrients to support photosynthesis (e.g., NH₄⁺, NO₃⁻, PO₄⁺) via direct absorption from the seawater and as an excretory byproduct of respiration (Hawkins & Klumpp, 1995; Toonen *et al.,* 2011). In return, zooxanthellae transfer photosynthetic carbon to the host in the form of glucose, glycerol, oligosaccharides and amino acids (Griffiths & Streamer, 1988; Ishikura *et al.,* 1999; Mies *et al.,* 2016).

Under natural conditions, the contribution of autotrophy to giant clam nutrition tends to increase with body size and has been shown to vary between species (Klumpp & Griffiths, 1994; Klumpp & Lucas, 1994; Hawkins & Klumpp, 1995). This may in part be related to differences in their characteristic habitats. For example, *T. derasa* and *T. mbalavuana,* two species which occur predominantly in clear, oceanic environments, derive most (*T. mbalavuana:* 70 percent at 28 m, 105 percent at 15 m), if not all (*T. derasa*), of the carbon required for growth and

respiration from autotrophy (Klumpp & Lucas, 1994). Notably, only *T. mbalavuana,* which is the deepestoccurring species of giant clam, increased its photosynthetic efficiency in the lowest light conditions (Klumpp & Lucas, 1994). *H. hippopus* and *T. gigas* exhibit a different strategy altogether, reflecting their natural occurrence in shallower intertidal and subtidal habitats, where there is often a higher concentration of suspended organics in the water column. Klumpp *et al.* (1992) showed that *T. gigas* is an efficient filter-feeder and that heterotrophic carbon supplied significant amounts of the total carbon necessary for its respiration and growth (65 percent in ∼43 mm individuals and 34 percent in ∼167 mm individuals). In a follow-up study, Klumpp and Griffiths (1994) similarly found that ingested carbon provided 61 to 113 percent of total needs in 40 to 80 mm *T. gigas* and 36 to 44 percent in *H. hippopus.* Some have hypothesized that differences in energy acquisition and expenditure may in part explain the growth and size differences among giant clam species, and in particular the enormous size of *T. gigas.* At this point, however, no clear nutritional basis for these differences has been resolved (Klumpp & Griffiths, 1994).

Giant clams associate with several Symbiodiniaceae genera, which can vary by geographic location (Fitt *et al.,* 1986). In the central Red Sea, for example, all sampled species (*T. maxima, T. squamosa, T. squamosina*) were found to exclusively harbor strains of *Symbiodinium* (formerly known as clade A) (Pappas *et al.,* 2017). In Okinawa, Japan, *T. squamosa* hosted varying communities of *Symbiodinium, Cladocopium* (formerly clade C), and *Durusdinium* (formerly clade D) (Ikeda *et al.,* 2017). Similarly, populations of *T. squamosa, T. maxima,* and *T. crocea* in eastern Indonesia were found to associate with mixed communities of these three genera (DeBoer *et al.,* 2012). While certain symbiont genera have been shown to confer physiological benefits to coral hosts (*e.g.,* greater tolerance to thermal stress or enhanced growth rate), there is no consistent evidence that these patterns translate directly to giant clams (reviewed in DeBoer *et al.,* 2012).

Growth and Reproduction

Giant clams are protandrous hermaphrodites, meaning they mature first as males and later develop ovaries to function as both male and female simultaneously (Wada, 1952; Rosewater, 1965). Size and age at maturity vary by species and geographic location, but

generally, giant clams are known to reach male phase maturity at around 2– 3 years of age (Heslinga *et al.,* 1984; Shelley, 1989) and female phase maturity as early as 3–5 years (Heslinga *et al.,* 1984; Isamu, 2008). In larger species, such as *T. gigas,* female maturity typically occurs later at around 8–9 years of age (Gomez & Mingoa-Licuanan, 2006). Giant clams reproduce via broadcast spawning, in which sperm and eggs are released into the water column where external fertilization takes place (Wada, 1954). Sperm is released first, followed by eggs after a short interval (Munro, 1993a).

Giant clams are exceptionally fecund, with individuals producing by many estimates tens to hundreds of millions of eggs during a single spawning event (Lucas, 1988). This number varies by species; for example, estimates suggest that *H. porcellanus* can release around 5 million eggs (Alca´zar *et al.,* 1987), *H. hippopus* can release 25–60 million eggs (Jameson, 1976; Alcala *et al.,* 1986), and *T. gigas* can release up to 500 million eggs (Crawford *et al.* 1986). However, despite their high fecundity, giant clams experience very high rates of mortality during early development (Jameson, 1976; Beckvar, 1981), resulting in very low levels of natural recruitment (Munro, 1993a). Reports suggest that less than 1 percent of all giant clam fertilized eggs survive larval development and progress to the juvenile phase in the wild (Jameson, 1976; Fitt *et al.,* 1984; Crawford *et al.,* 1986). As Lucas (1994) describes, ''the extreme example is *T. gigas,* which being at or near the pinnacle of fecundity, must have near the lowest level of survival of potential recruits in the animal kingdom.''

Many have described giant clam recruitment as ''erratic'' (McKoy *et al.,* 1980; Adams *et al.,* 1988; Lucas, 1994; Guest *et al.,* 2008). For example, Braley (1988) observed ''extremely low'' average recruitment on the Great Barrier Reef, punctuated by a major recruitment event in 1987, which yielded the largest population of *T. gigas* that had been recorded at the time. This pattern aligns with the concept of 'sweepstakes' reproduction, which is the chance matching of reproductive activity with oceanographic conditions conducive to spawning, fertilization, dispersal, and successful recruitment (Hedgecock, 1994). This can lead to sporadic waves of recruitment depending on the prevailing oceanographic conditions facilitating fertilization and carrying a successful cohort of 'sweepstakes' larvae to a suitable settlement location. Importantly, for broadcast spawning organisms like giant clams, which

primarily rely on the mixing of gametes with neighboring individuals, this reproductive strategy can be especially sensitive to changes in population density. In particular, low abundance and low population density severely reduces the likelihood of such sweepstakes success by minimizing the chance of fertilization.

There is considerable variation in the frequency and seasonality of spawning events among giant clam species. There is no evidence of reproductive seasonality in the central tropics, with some populations possessing ripe gametes year-round (Heslinga *et al.,* 1984; Munro, 1993a; Lindsay *et al.,* 2004). At higher latitudes, spawning is most often associated with late spring and summer months and can occur once per year (Shelley & Southgate, 1988) or in some cases periodically over the course of several months (Fitt & Trench, 1981; Heslinga *et al.,* 1984; Roa-Quiaoit, 2005). The environmental cues that initiate gamete release are not fully understood, but there is evidence that the lunar cycle may play a critical role. In Palau, for example, 76 percent and 24 percent of 55 observed spawning events by *T. gigas* occurred during the second and fourth quarter of the lunar cycle, respectively (Heslinga *et al.,* 1984). Unlike many other broadcast spawning organisms, there is little evidence that temperature is important for the induction of spawning (Wada, 1954; Fitt & Trench, 1981).

Once one or more clams have begun to spawn, chemical cues associated with egg release have been shown to play a role in triggering the spawning of nearby individuals, which then release sperm for fertilization (Munro, 1993a). While a maximum distance between spawning individuals has not been quantified (Neo *et al.,* 2015), in situ observations by Braley (1984) showed that 70 percent of the nearest spawning neighbors were within 9 m of one another, while only 13 percent were between 20–30 m of one another. Through laboratory trials, Neo *et al.* (2015) found that gametes of *T. squamosa* remained viable for up to 8 hours, but that viability decreased significantly with time. Because of these factors, maintaining sufficient population densities to facilitate fertilization among neighboring individuals is vital to the persistence of giant clam populations.

Importantly, there is also some evidence that giant clams are able to self-fertilize with varying fitness consequences among different species. After observing that the end of sperm release occasionally overlaps with the beginning of egg release in certain giant clam species (see also Kurihara *et al.*

(2010)), Murakoshi and Hirata (1993) experimentally induced self-fertilization in four species of giant clams (*H. hippopus, T. crocea, T. maxima,* and *T. squamosa*) by removing the gonads and mixing gametes. They found that all four species are capable of selffertilization, but that larval development of *H. hippopus* was significantly altered, and no *T. maxima* juveniles metamorphosed completely to the normal pediveliger stage. Juvenile *T. crocea* and *T. squamosa* survived up to a year post-fertilization, but the study was not long enough to evaluate possible effects on reproductive maturity or later-phase development. More recently, Zhang *et al.* (2020) evaluated the fitness effects of selffertilization in three species of giant clams (*T. crocea, T. derasa,* and *T. squamosa*) after 1 year of development. They found that there was no effect of self-fertilization on the fertilization rate or zygotic fertility in any species. Larval survival and growth rate was significantly reduced in *T. crocea* and *T. squamosa,* but not *T. derasa.* However, while self-fertilization may be possible in some species, numerous accounts of spawning in culture and in situ suggest that sperm and eggs are released successively without an overlap in timing in the vast majority of spawning events (LaBarbera, 1975; McKoy, 1980; Wada, 1954). It is likely that this limits the occurrence of self-fertilization in nature and minimizes its role in giant clam productivity.

Once an egg is fertilized, the life cycle of giant clams is typical of bivalve molluscs (Lucas, 1994; Soo & Todd, 2014). Fertilized eggs are approximately 90–130 µm in diameter (Jameson, 1976) and have a slight negative buoyancy. They usually develop into swimming trochophores within 12–24 hours, at which time they are able to alter their depth distribution and begin searching for an eventual settlement site (Ellis, 1997; Neo *et al.,* 2015). Shell production in molluscs begins at this early phase of development, following a thickening of epithelial cells that will define the future shell field (Gazeau *et al.,* 2013). Within 36–48 hours after fertilization, larvae develop into shelled, swimming veligers, which use a ciliated velum for locomotion and feeding (Soo & Todd, 2014). The veligers are highly motile and begin feeding on microalgae of up to 10 µm in diameter (Munro, 1993a). Over the course of several days, the velum begins to degenerate and a foot develops as the larvae transition into the pediveliger stage (Soo & Todd, 2014). At this point, larvae alternate between swimming and crawling on the

substrate, using their foot for sensing and feeding (Lucas, 1988; Soo & Todd, 2014). Pediveligers generally develop 6– 14 days post-fertilization; however, Fitt and Trench (1981) noted considerable variation in the timing of this transition, where most took place by day 10 but others were observed up to 29 days post-fertilization.

Larvae metamorphose into juvenile clams at an approximate size of 200 μ m (LaBarbera, 1975; Lucas, 1988; Soo & Todd, 2014). Juvenile clams remain mobile and are able to crawl both horizontally and vertically using their foot as they search for a settlement location (Soo & Todd, 2014). Giant clam larvae tend to settle on substrates that offer shelter in the form of grooves and crevices, highlighting the importance of habitat rugosity during this stage of development (Soo & Todd, 2014). Additionally, juveniles have been observed to move non-randomly and clump towards conspecifics, which some hypothesize may be a behavioral adaptation to enhance reproduction and predator defense (Huang *et al.,* 2007; Neo, 2020). Juvenile clams eventually attach themselves to the substrate by use of byssal threads, which in some species will remain in place throughout their lifetime. Larger species typically lose the byssal threads after reaching adulthood and are held in place by their size and weight (Lucas, 1988).

Growth rates vary among species, with larger species exhibiting more rapid growth than smaller species (Munro & Heslinga, 1983; Lucas, 1988). Growth rates after settlement generally follow a sigmoid ("S" shaped) curve, beginning slowly, then accelerating after approximately 1 year and slowing again as the animals approach sexual maturity (Lucas, 1988; Ellis, 1997). Lucas (1994) provides examples of maximum rates of monthly shell growth for several species as recorded under culture conditions in the Philippines: *H. hippopus*—5.3 mm, *T. squamosa*—4.5 mm, *T. derasa*—5.6 mm, and *T. gigas*—9.1 mm (Calumpong, 1992; Gomez & Mingoa, 1993). Shell growth continues throughout the clam's lifespan (Lucas, 1994).

The maximum lifespan of giant clams is not known, but the oldest reliably aged individual was a large *T. gigas* determined to be 63 years old (Lucas, 1994). Similar aging studies based on the analysis of growth rings in the shell estimated a 43 cm-long *T. squamosa* to be around 22 years old (Basker, 1991), a ∼20 cm-long *T. maxima* to be around 28 years old (Romanek *et al.,* 1987), and a 93 cm-long *T. gigas* to be around 60 years old (Watanabe *et al.,* 2004). Using growth and mortality estimates, Dolorosa *et al.* (2014) predicted a

lifespan of more than 20 years for *H. porcellanus.*

Population Structure

Current literature indicates several consistent features of giant clam population genetics throughout their range. The first is significant genetic differentiation between giant clam populations of the central Pacific region, including Kiribati, Marshall Islands, Tuvalu and Cook Islands, and the western Pacific region, including the Great Barrier Reef, Philippines, Solomon Islands and Fiji (Benzie & Williams, 1995, 1997). The pattern is consistent across *T. gigas* and *T. maxima,* although there is some variability in the inferred level of connectivity between the Great Barrier Reef and Philippines in *T. derasa* (Macaranas *et al.,* 1992). Interestingly, the patterns of genetic connectivity do not reflect oceanic currents as would be expected for a passively-dispersing organism like giant clams. Hence, Benzie and Williams (1997) hypothesize that ''other mechanisms dominate present-day dispersal, or that [the observed patterns] reflect past connectivity which present-day dispersal along major surface currents has not altered over thousands of years.''

Other studies describe a relatively consistent pattern of genetic structure within the Indo-Pacific region, often highlighting four or five genetic clusters distinguishing populations of the Red Sea, Western Indian Ocean, Eastern Indian Ocean, Indo-Malay Archipelago, and Western Pacific. In every case, populations of *T. squamosa* and *T. maxima* in the Red Sea are found to be highly divergent from all other populations in their range (Nuryanto & Kochzius, 2009; Huelsken *et al.,* 2013; Hui *et al.,* 2016; Pappas *et al.,* 2017; Lim *et al.,* 2018). The same is true of Western Indian Ocean populations, though to a slightly lesser extent (Hui *et al.,* 2016; Lim *et al.,* 2018). Additionally, there is a uniform pattern of differentiation between giant clam populations in the Indo-Malay Archipelago and those in the eastern Indian Ocean and Java Sea (Kochzius & Nuryanto, 2008; Nuryanto & Kochzius, 2009; Huelsken *et al.,* 2013; Hui *et al.,* 2016). This pattern is largely consistent across *T. squamosa, T. maxima,* and *T. crocea,* although some studies note variability between species with respect to certain genetic breaks identified in the Java Sea and in Chendewasih Bay (Nuryanto & Kochzius, 2009; Huelsken *et al.,* 2013). Population genetic data from *T. maxima* and *T. crocea* (species which are not subject to this rulemaking) suggest that

there may also be genetic breaks between the western Pacific islands and Indo-Malay Archipelago (Nuryanto & Kochzius, 2009; Huelsken *et al.,* 2013; Hui *et al.,* 2016). However, similar data are not available for any of the seven species considered here.

On a smaller scale, giant clam populations within the northern and central Great Barrier Reef exhibit high genetic connectivity (Benzie & Williams, 1992, 1995, 1997). Evans and Jerry (2006) found tenuous evidence of isolation-by-distance in this region, which would suggest that populations may be connected by the prevailing southward flow of the East Australian Current. In contrast, Kittiwattanawong *et al.* (2001) found that *T. squamosa* in the Andaman Sea are genetically distinct from those in the Gulf of Thailand, likely due to the physical barrier of the Malay Peninsula minimizing dispersal between these populations.

Current and Historical Distribution and Population Abundance

There are no current or historical estimates of global abundance for any of the seven giant clam species considered here. Therefore, we rely on the best available scientific and commercial data, including formal and informal survey data, qualitative descriptions of abundance or population trends, and anecdotal reports from specific sites, to evaluate the status of each species in each country, territory, or region throughout its range.

Much of the information used to determine the status of each species is derived from Table 4 of Neo *et al.* (2017), which we have supplemented or revised based on more recent survey data or reports. We have also adjusted the criteria used to define each qualitative abundance category, which Neo *et al.* (2017) had previously defined as follows: Abundant: >100 individuals (ind) ha⁻¹, Frequent: $1-10$ ind ha⁻¹, Rare: < 0.1 ind ha⁻¹. In doing so, we considered the reproductive ecology of giant clams, and in particular, the observations of Braley (1984) regarding the distance between nearest-spawning *T. gigas* during a natural spawning event. Braley (1984) measured that 70 percent of nearest-spawning individuals were within 9 m of one another, while only 13 percent were between 20–30 m of one another, suggesting that spawning synchrony decreases with distance. As broadcast spawning organisms, giant clams rely on sufficient population density in order to facilitate successful external fertilization of their gametes. Based on the distances above, we determined the minimum

population density in a 1-hectare (10,000 m2) square grid in which individuals could be evenly spaced at 9 and 30 m apart. Respectively, these distances represent populations that we consider to be ''Abundant,'' where we expect relatively high reproductive success, and ''Frequent,'' where we expect lower but moderate reproductive success. A ''Rare'' population in which individuals are spaced farther than 30 m apart on average is likely to have infrequent, sporadic reproductive success. This approach led to the following criteria: Abundant: >100 ind ha–1 (9-m distance), Frequent: 10–100 ind ha–1 (30-m distance), and Rare: <10 ind ha–1 (>30-m distance).

Importantly, precise quantitative assessments of abundance are not possible in most instances, as many regions lack current or comprehensive survey data (see the accompanying Status Review Report for all reported estimates of population density from specific surveys). Thus, where survey data are limited to only a few sites or where recent survey data are not available, we also take into account other available information, including qualitative descriptions of abundance or population trends, to reach a determination on the likely status of the species throughout each country, territory, or region in its entirety. In other words, although survey data from a single site may indicate a relatively abundant population, if the species is considered absent from all other areas, the species may be considered ''frequent'' or ''rare'' on average in that location. This methodology generally follows the approach used by Neo *et al.* (2017)

Additionally, it is important to note that, in the interest of simplicity, these qualitative abundance categories are based on an assumption of uniform spacing between individuals. However, a number of studies report that giant clams often occur in a clumped distribution, where individuals are concentrated in a number of small, distantly-separated groups. In these cases, the abundance categories may underestimate the productivity of the respective population. In other words, if survey data indicate that a species occurs in some location at low abundance on average, reproductive success is more likely if the individuals are clustered in a few small groups, minimizing the distance between neighboring individuals, than if they are spread uniformly across the seafloor.

In table 1 below, we summarize the status of each species in each of the locations where it has been observed. Full narrative descriptions of the data and scientific studies that informed the be found in the accompanying Status following abundance assessments can Review Report (Rippe et al., 2023).

TABLE 1-SUMMARY OF THE POPULATION STATUS FOR EACH OF THE SEVEN GIANT CLAM SPECIES IN ALL COUNTRIES, TERRITORIES, AND REGIONS WHERE THEY HAVE BEEN OBSERVED (ADAPTED FROM NEO et al., 2017 AND SUPPLE-MENTED WITH MORE RECENT INFORMATION WHERE AVAILABLE)

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TABLE 1—SUMMARY OF THE POPULATION STATUS FOR EACH OF THE SEVEN GIANT CLAM SPECIES IN ALL COUNTRIES, TERRITORIES, AND REGIONS WHERE THEY HAVE BEEN OBSERVED (ADAPTED FROM NEO *et al.,* 2017 AND SUPPLE-MENTED WITH MORE RECENT INFORMATION WHERE AVAILABLE)—Continued

Note: Species abundance categories are as follows. +++: Abundant (>100 ind ha–1), ++: Frequent (10–100 ind ha–1), +: Rare (<10 ind ha–1), -: Locally extinct, *INT:* Introduced to non-native location; *REIN:* Reintroduced (cultured specimens) to locations where the species had previously been extirpated; *dd:* Data Deficient (*i.e.,* reports of species presence are not confirmed). Empty cells indicate locations where a species

has not been observed.
¹ Species names are abbreviated as follows: HH: *H. hippopus,* HP: *H. porcellanus,* TD: *T. derasa,* TG: *T. gigas,* TMB: *T. mbalavuana,* TS: *T. squamosa,* TSI: *T. squamosina.*

Extinction Risk Analysis

Methods

In determining the extinction risk of each species, it is important to consider both the demographic risks facing the species, as well as current and potential threats that may affect the species' status. To this end, the status review synthesized the best available scientific and commercial data regarding the five threat categories listed in section 4(a)(1) of the ESA. These are: (1) the present or threatened destruction, modification, or curtailment of its habitat or range; (2) overutilization for commercial, recreational, scientific, or educational purposes; (3) disease or predation; (4) inadequacy of existing regulatory mechanisms; or (5) other natural or manmade factors affecting its continued existence. Second, we conducted a demographic risk analysis following the Viable Population (VP) approach derived from McElhany *et al.* (2000), which addresses four biological descriptors of species status: abundance, productivity (*i.e.,* population growth rate), spatial distribution, and diversity. The VP approach reflects concepts that are well-founded in conservation biology and considers demographic factors that individually and collectively provide strong indicators of extinction risk. It is designed to both capture the biological symptoms of past threats that have contributed to the species' current status and provide insight into how the species may respond to present and future threats.

With respect to each threat and each demographic risk factor, we assigned a qualitative score from 1 to 5 representing its estimated contribution to the species' extinction risk (''very low," "low," "moderate," "high," or ''very high'' risk). Detailed definitions of these risk levels can be found in the

accompanying Status Review Report. We also assigned a confidence rating from 0 to 3, reflecting the quantity and quality of information used to assign the score, as follows: 0 = No confidence (*i.e.,* no available information); 1 = Low confidence (*i.e.,* very limited available information); 2 = Medium confidence (*i.e.,* some reliable information available, but reasonable inference and extrapolation is required); 3 = High confidence (*i.e.,* reliable information with little or no extrapolation or inference required).

Lastly, all information from the threats assessment and demographic risk analysis was synthesized to estimate the overall risk of extinction for each species. For this analysis, we used three reference levels of extinction risk (''low,'' ''moderate,'' and ''high''), which are consistent with those used in prior ESA status reviews. ''Low'' risk indicates a species that is not at a moderate or high level of extinction risk (see ''Moderate'' and ''High'' risk below). A species may be at a low risk of extinction if it is not facing threats that result in declining trends in abundance, productivity, spatial structure, or diversity. A species at low risk of extinction is likely to show stable or increasing trends in abundance and productivity with connected, diverse populations. ''Moderate'' risk indicates a species that is on a trajectory that puts it at a high level of extinction risk in the foreseeable future (see ''High'' risk below). A species may be at moderate risk of extinction due to projected threats or declining trends in abundance, productivity, spatial structure, or diversity. "High" risk indicates a species that is at or near a level of abundance, productivity, spatial structure, and/or diversity that places its continued persistence in question. The demographics of a species at such a high

level of risk may be highly uncertain and strongly influenced by stochastic or depensatory processes. Similarly, a species may be at high risk of extinction if it faces clear and present threats (*e.g.,* confinement to a small geographic area; imminent destruction, modification, or curtailment of its habitat; or disease epidemic) that are likely to create present and substantial demographic risks.

Importantly, these extinction risk categories are not meant to be a direct translation of the final listing determination for the species, as listing determinations must also consider ongoing conservation efforts of any State, foreign nation, or political subdivision thereof (16 U.S.C. 1533(b)(1)(A)) to determine whether the species meets the ESA's definition of an ''endangered species'' or ''threatened species.'' Rather, the extinction risk assessment in the Status Review Report represents the scientific conclusion about the overall risk of extinction faced by the species under present conditions and in the foreseeable future based on an evaluation of the species' demographic risks and assessment of threats.

Defining the ''*Foreseeable Future*''

The appropriate time horizon for evaluating whether a species is more likely than not to be at a high level of risk in the ''foreseeable future'' varies on a case-by-case basis. For example, the time horizon may reflect certain life history characteristics (*e.g.,* long generation time or late age-at-maturity) and the time scale over which identified threats are likely to impact the biological status of the species. In other words, the foreseeable future represents the period of time over which we can reasonably determine that both future threats and the species' response to

those threats are likely. *See generally* 50 CFR 424.11(d). It does not necessarily need to be limited to the period that the species' status can be quantitatively modeled or predicted within predetermined limits of statistical confidence. Reliable projections may be qualitative in nature.

With these criteria in mind, we determined that the ''foreseeable future'' for the following extinction risk analyses spans approximately ∼50–60 years. Based on what is known about the life history traits of giant clams, with longevity estimated to be at least 50 years (up to 60 years for *T. gigas*), maturity ranges from 3 to 9 years, and exceedingly low recruitment, it would likely take at least this amount of time (*i.e.,* multiple generations) for the effects of any management actions to be realized and reflected in population abundance indices. Similarly, the impact of present threats to the species would be realized in the form of noticeable population declines within this timeframe, as has been demonstrated in the available literature. As the primary operative threats to giant clams are overutilization for subsistence and commercial harvest, this timeframe would allow for reliable predictions regarding the impact of current levels of harvest-related mortality on the biological status of all the species.

One important exception to this timeframe is in regard to the future impacts and threats related to climate change. Based on the current standard for climate projections, under which most available models are extended to the end of the century, we use the same timeframe (*i.e.,* present day–2100) to define the ''foreseeable future'' in assessing the likely future threat of climate-related habitat degradation and climate-related impacts to giant clam fitness.

Threats Assessment

Below, we describe the natural and anthropogenic threats to each of the seven giant clam species within the framework of the five threat categories outlined in section 4(a)(1) of the ESA. Because a number of species occupy overlapping ranges and often co-occur in similar habitats, certain threats may apply to more than one species. In each section, we highlight the severity of the threat to each of the species affected and provide additional species-specific information where appropriate. Additional details may be found in the Status Review Report (Rippe *et al.,* 2023).

The Present or Threatened Destruction, Modification, or Curtailment of Its Habitat or Range

As is mentioned in the species descriptions above, giant clams are often closely associated with coral reefs, inhabiting all types of shallow-water reef ecosystems (*i.e.,* fringing, barrier and atoll reefs), as well as various reefadjacent habitats. However, there is no conclusive evidence that giant clams directly rely on live, pristine corals for their survival. Certain species are habitat generalists (*e.g., T. squamosa, T. gigas*)—they are often observed among live corals but can also be found in other habitats, which are not pristine coral reef (*e.g.,* sand, rock, dead coral rubble, seagrass beds, macroalgae zones). Others are more specialized—*T. mbalavuana* is found exclusively at depth on reef slopes, *T. derasa* is found predominantly in offshore coral reef areas, while *H. hippopus, H. porcellanus* and *T. squamosina* tend to prefer sandy areas, shallow lagoon flats and seagrass beds adjacent to coral reefs.

Available research on larval settlement preference offers some clues as to what may be driving the association with coral reefs. Several studies show that *T. squamosa* larvae prefer to settle on substrates of relatively high rugosity and are drawn to crustose coralline algae (CCA), but actively avoid settling on live coral (Courtois de Vicose, 2000; Calumpong *et al.,* 2003; Neo *et al.,* 2009). Additionally, the small giant clam (*T. maxima*) has shown an ability to discriminate between ''favorable'' and ''unfavorable'' habitats, preferring to settle near the effluent of conspecifics and near the effluent of live coral and CCA, rather than cyanobacteria and sponges (Dumas *et al.,* 2014). However, this information is limited to only one of the seven species being analyzed in connection with this proposed rule, and there are no such data for species that are predominantly found in sand flats and seagrass beds, where rugosity is especially low and settlement cues might differ.

Based on the known features of giant clam biology and larval development, Lucas *et al.* (1989) hypothesized that the proximity of giant clams to coral reefs is, to some extent, a result of two environmental requirements, which are maximized in shallow reef habitats: (1) high light conditions to support the photosynthetic nutrition that giant clams derive from their algal symbionts, and (2) substrate rugosity to provide cryptic settlement locations for vulnerable recruits and juveniles. While we cannot conclude that these factors are equally important to all species of

giant clams, it is within the context of these two habitat requirements that we discuss the following threats to coral reef ecosystems and their potential impacts to giant clams.

Climate Change Impacts to Coral Reefs

Reef-building corals typically occur in waters that range between 25 °C–30 °C and are highly sensitive to temperature excursions outside of this range (Brainard *et al.,* 2011). Prolonged exposure to high temperature anomalies can lead to coral bleaching, where the coral host expels its symbiotic zooxanthellae, leaving the tissue translucent and revealing its white skeleton underneath. Bleachingassociated mortality is quite variable and can depend on the duration and intensity of elevated temperatures, geographic location, bleaching history, species present, and other factors (Pandolfi *et al.,* 2011; Putnam & Edmunds, 2011; van Hooidonk & Huber, 2012). Mild to moderate bleaching does not always lead to death; however, repeated and prolonged bleaching can cause widespread coral mortality on regional or global scales. Extreme summer temperature anomalies associated with strong El Niño events have led to three recognized global bleaching events in 1997–98, 2009–10 and 2014–17 (Hughes, Kerry, *et al.,* 2017; Lough *et al.,* 2018; Eakin *et al.,* 2019). The latest (2014–17) was the longest and most severe global bleaching event in recorded history. It affected every major coral reef region and led to the mortality of one third of the Great Barrier Reef in Australia (Couch *et al.,* 2017; Hughes, Kerry, *et al.,* 2017; Hughes, Kerry, *et al.,* 2018). In addition, many other regional-scale bleaching events over the last several decades have caused widespread coral mortality in reef communities throughout the Indo-Pacific (Brainard *et al.,* 2011; Hughes, Anderson, *et al.,* 2018).

While coral bleaching patterns can be complex, there is a general consensus that rising global ocean temperatures have led to more frequent and severe coral bleaching and mortality events (Hughes, Anderson, *et al.,* 2018; Lough *et al.,* 2018). Without drastic action to curb greenhouse gas emissions, this trend is projected to continue throughout this century (van Hooidonk *et al.,* 2016). Additionally, several studies have shown that warming can significantly increase coral susceptibility to disease (Bruno *et al.,* 2007; Sokolow, 2009; Brainard *et al.,* 2011; Howells *et al.,* 2020). The combination of these warming-related impacts has already caused dramatic

declines in many coral species and changes to the composition and structure of coral reefs around the world (Brainard *et al.,* 2011; Hughes, Barnes, *et al.,* 2017; Hughes, Kerry, *et al.,* 2018). During the major 2016 coral bleaching event on the Great Barrier Reef, for example, the fast-growing, structurally complex tabular and branching species suffered disproportionately (≤75 percent mortality on heavily bleached reefs), shifting reef communities towards taxa with simpler morphological characteristics and slower growth rates (Hughes, Kerry, *et al.,* 2018). Other studies similarly suggest that coral reef ecosystems, rather than disappear entirely as a result of warming, will likely persist, but with unpredictable changes to their community composition and ecological function (Pandolfi *et al.,* 2011; Hughes *et al.,* 2012).

Coral reefs are also facing increasing risk from ocean acidification, the process by which atmospheric carbon dioxide $(CO₂)$ is absorbed into the surface ocean, resulting in reduced seawater pH and reduced availability of carbonate ions. Due to anthropogenic $CO₂$ emissions, average surface ocean pH (total scale, pHt) has already decreased by more than 0.1 pHt units below the pre-industrial average of 8.17, and is expected to fall up to an additional 0.42 pHt units by 2100 under the worst-case emissions scenario from the Intergovernmental Panel on Climate Change (IPCC) (RCP 8.5) (Pörtner *et al.*, 2014).

Such reductions in ocean pH could lead to drastic changes to the net calcification balance in many coral reef ecosystems. Numerous laboratory and mesocosm experiments have demonstrated a correlation between lower pH (or elevated partial pressure of CO2, pCO2) and decreased coral calcification rates (Anthony *et al.,* 2008; Ries *et al.,* 2009; Anthony *et al.,* 2011; Gazeau *et al.,* 2013; Albright *et al.,* 2018). Brainard *et al.* (2011) provide a table summarizing the existing literature on the topic (table 3.2.2 of the report), and for every species studied, net calcification rate either declines, or in very few, there is no significant effect. In a pair of controlled mesocosm experiments, net community calcification of a small enclosed coral reef was found to increase under enhanced alkalinity and decrease after the addition of CO₂ (Albright *et al.*, 2016; Albright *et al.,* 2018), indicating that current levels of acidification are already impairing ecosystem-level calcification and will likely exacerbate this effect in the future. Coupled with dwindling coral cover due to warming-

associated bleaching and mortality, continued acidification could transition many reef systems from net overall accretion to net erosion within this century (Eyre *et al.,* 2018; Cornwall *et al.,* 2021).

Others anticipate that ocean acidification will also weaken the structural integrity of coral reefs, both by promoting the efficiency of bioeroding organisms and by reducing reef cementation (*i.e.,* secondary processes of carbonate precipitation that bind the reef framework). Observations from coral reefs of the eastern Pacific, which occur in naturally low-pH upwelling zones reveal some of the highest rates of bioerosion documented globally, as well as poorly cemented, fragile, and unstable reef frameworks (Glynn, 1988; Eakin, 1996, 2001; Manzello *et al.,* 2008). Crustose coralline algae (CCA) contribute significantly to reef cementation by consolidating loose rubble and sealing porous dead coral skeletons (Adey, 1998; Littler & Littler, 2013). There is major concern that CCA may be among the most sensitive taxa to declines in seawater pH, because they build their skeletons with magnesium-rich calcite, a highly soluble form of carbonate (Andersson *et al.,* 2008). Although some argue that the risk to CCA may be overestimated, as certain aspects of their skeletal structure and biology have proven resilient to projected future conditions (Nash *et al.,* 2013; Nash *et al.,* 2015; Nash *et al.,* 2016). At this point, the potential impacts of ocean acidification on CCA are not fully resolved.

Given the documented and projected impacts of ocean warming and acidification on coral reef ecosystems, we assessed the direct implications of these impacts on the extinction risk of the seven giant clam species. In our previous status review for 82 species of corals, Brainard *et al.* (2011) concluded that ''the combined direct and indirect effects of rising temperature, including increased incidence of disease, and ocean acidification [. . .] are likely to represent the greatest risks of extinction to all or most of the candidate coral species over the next century.'' They assessed the threat of continued ocean warming to be ''highly certain'' and graded the threat as ''high'' for most regions where the candidate corals are known to occur. Based on this assessment, we find it likely that live coral cover in general will continue to decline due to more frequent and severe bleaching events, and that ecosystemscale calcification rates will decline as a result. Critically for giant clams, the negative impacts of warming are most

pronounced in the fast-growing branching and tabular coral species, which are the primary contributors to the three-dimensional complexity of reef habitats. Thus, continued loss of live coral cover and of these coral species in particular will likely severely reduce the rugosity of future reef ecosystems. There is also evidence that ocean acidification will further inhibit calcification rates of living corals and weaken the structural integrity of the reef framework, although the magnitude of these effects is not clear. As with ocean warming, the primary implication of these effects for giant clams will be reduced habitat rugosity.

Nevertheless, there are two important layers of uncertainty associated with these predictions, and especially their potential impacts to giant clam habitat. First, with respect to ocean acidification, carbonate chemistry is notoriously difficult to model precisely in open systems, as it relies on many physical and biological factors, including seawater temperature, proximity to land-based runoff and CO2 seeps, proximity to sources of oceanic CO2, salinity, nutrients, as well as ecosystem-level photosynthesis and respiration rates. The last factor, in particular, means that in many cases, daily fluctuations in pH or carbonate chemistry can significantly outweigh projected long-term changes to the average (Manzello *et al.,* 2012; Johnson *et al.,* 2019). Secondly, as mentioned above, there is very little research establishing the degree to which giant clams rely on coral reef rugosity and thus might be impacted by any reduction thereof. The few larval choice experiments to date suggest that *T. squamosa* prefers rough to smooth surfaces and is attracted to CCA. However, most giant clam species can be found in an array of habitat types, and some even seem to prefer areas of low rugosity, such as sand flats and seagrass beds (*e.g., H. hippopus, H. porcellanus,* and *T. squamosina*). No studies have quantified how or if giant clams might be affected under varying levels of coral reef complexity.

If giant clams are sensitive to reductions in net ecosystem calcification and reef rugosity, the projected climate change-related impacts to coral reefs would likely pose a significant threat to *T. derasa, T. gigas, T. mbalavuana,* and *T. squamosa* within the foreseeable future, as these species are known to inhabit coral reef environments. We would expect decreased larval recruitment and juvenile survival across broad portions of their range. These early life stages are already known to suffer exceptionally

high mortality rates naturally, and any further reduction in productivity would greatly threaten the viability of remaining giant clam populations.

However, without more information on the direct association between substrate rugosity and giant clam survival and productivity, it is difficult to estimate with any confidence the degree to which reef rugosity must decline to threaten the persistence of these species. Likewise, given the lingering uncertainty in the dynamics and effects of ocean acidification, it is not possible to estimate a timespan over which such a risk can be expected. Thus, while it is likely that continued ocean warming and acidification will drastically alter coral reef communities and reduce the rugosity of many reef habitats, we concluded that the potential effect on the quality or suitability of giant clam habitat cannot be confidently assessed.

Coastal Development

The physical degradation of nearshore habitats due to coastal development poses an additional threat to giant clams throughout much of their range. Sedimentation associated with the construction and maintenance of coastal infrastructure can reduce the amount of suitable substrate available for larval settlement. There is extensive evidence for such an effect in corals—increased sediment load has been shown to deter larval recruitment (Babcock & Davies, 1991), reduce settlement success and survival (Hodgson, 1990; Babcock & Smith, 2002), and decrease the effectiveness of CCA to induce settlement (Ricardo *et al.,* 2017). We could not find any research directly investigating this effect in giant clams; however, similarities in the biology and behavior of giant clam larvae would suggest that comparable results can reasonably be expected. Like coral larvae, giant clam larvae prefer rough settlement surfaces and are likely deterred by unconsolidated, finegrained silt that is typical of anthropogenic sedimentation. Moreover, CCA provide a similarly important settlement cue for giant clams (Courtois de Vicose, 2000; Neo *et al.,* 2009; Neo *et al.,* 2015), and a reduction in effectiveness would likely decrease larval recruitment and settlement success.

Importantly, compared to habitat degradation due to climate change, coastal development poses a more localized threat to giant clam populations in specific regions. In the Red Sea, for example, Roa-Quiaoit (2005) notes intense modification to the Jordanian coastline over ''four decades

of rampant development of ports, industrial and tourism areas, as well as extreme events such as oil spills.'' Surveys of giant clam density in the area revealed an inverse relationship between the population density of *T. squamosa* and metrics of human impact and coastal use. The author argues that the observed 12-fold reduction of giant clam density in Jordan over three decades is in major part due to this intense habitat modification. Similar examples of anthropogenic impacts to the coastal environment have also been documented in many areas of the Indo-Pacific region, although this is often discussed in relation to the health of coral reef ecosystems. In Singapore, approximately 60 percent coral reef area was lost during the 20th century due to land reclamation and associated sedimentation (Chou, 2006; Guest *et al.,* 2008). On three specific Singapore reefs—Tanjong Teritip, Pulau Seringat, and Terumbu Bayan—Neo and Todd (2012) note that giant clams were once found, but the areas have since been reclaimed (covered over) in their entirety. In addition, more than 20 percent of coral reefs in Indonesia, 35 percent of reefs in Malaysia, 25 percent of reefs in Papua New Guinea, and 60 percent of reefs in the Philippines are threatened by the impacts of coastal development, including runoff from construction and waste from coastal communities (Burke *et al.,* 2012).

In addition to undergoing intense coastal development activities over the past several decades, many of these areas are not well regulated with respect to coastal runoff and often do not prioritize sustainable management of the coastal environment (*e.g.,* Gladstone *et al.,* 1999; O. A. Lee, 2010). In contrast, the Great Barrier Reef in Australia and island nations of the central and western Pacific, two other important areas of giant clam distribution, likely do not suffer the same effects of coastal development. Australia strictly enforces an integrated management plan to protect the Great Barrier Reef from the effects of coastal land use change via numerous national and State regulations, and the relatively small populations of most Pacific island nations minimize the impact of coastal development on surrounding waters.

Because *T. mbalavuana* and *T. derasa* reside preferentially in offshore coral reef areas, we conclude that habitat degradation of the nearshore environment related to coastal development likely does not pose a significant threat to these two species. With respect to *H. hippopus, T. gigas,* and *T. squamosa,* considering the relatively localized impacts of coastal

development (*e.g.,* near heavily urbanized areas) compared to the size of the species' ranges, we conclude that the threat of habitat destruction, modification, or curtailment related to nearshore impacts of coastal development likely poses a low risk to *H. hippopus* and *T. gigas,* and a very low risk to *T. squamosa.* Specifically, we find the risk to be lower for *T. squamosa* due to the species' expansive geographic range as well as its current abundance and distribution, compared to *H. hippopus* and *T. gigas.*

Because the restricted range of *H. porcellanus* is centered in a region of intense urban development (*i.e.,* within the densely populated Indo-Malay Archipelago), we conclude that habitat destruction and modification of the nearshore environment poses a moderate risk to the species. In other words, it likely contributes significantly to the species' long-term extinction risk, but given the localized nature of these impacts, does not in itself constitute a danger of extinction in the near future. *H. porcellanus* is also faced with an acute threat of habitat destruction in the northern portion of its range, where fishermen primarily from Tanmen, China have been razing shallow reef areas of the South China Sea in a search for giant clam shells (see *Tanmen Destructive Shell Harvesting* below). The damage from these operations is extensive and has likely eliminated any *H. porcellanus* that may have previously occurred in the islands of the South China Sea.

With respect to *T. squamosina,* we considered reports indicating specific areas of the Red Sea coastline which have been targeted for development of tourist activities and infrastructure, including Hurghada and the Gulf of Aqaba coastline from Sharm el-Sheikh to Nuweiba (Egypt), Eilat (Israel), and Aqaba (Jordan). These areas are significant, as they directly overlap with the majority of recent *T. squamosina* observations. As is mentioned above, Roa-Quiaoit (2005) estimated that 70 percent of the Jordanian coastline has been developed into ports, industrial centers, and tourism areas over the past several decades. Additionally, near Hurghada, Mekawy and Madkour (2012) observed dredging activities associated with a newly-constructed harbor and offshore trash disposal from boats. The authors also described industrial and tourist activities in several other areas along the coast of mainland Egypt (*e.g.,* oil drilling in El-Esh, dense industrial and tourism-related development near Safaga Harbor, high human activity in Quesir), which they argue have likely been the principal factors driving the

declining abundance of giant clams (primarily *T. maxima*) in these areas. Similarly, Hassan *et al.* (2002) reported ''major decreases in giant clam populations between 1997 and 2002, with many small clams seen in 1997 not surviving through to 2002.'' The authors attributed this population loss directly to sedimentation from major construction activities in South Sinai. While these studies address impacts to giant clams broadly, it is likely that *T. squamosina* experiences a similar threat in these areas. Lastly, Pappas *et al.* (2017) suggest that coastal development may, in combination with overutilization, explain the apparent absence of *T. squamosina* in the central Red Sea, but do not provide any data to support this claim.

Thus, while we do not have any data specifically linking habitat destruction, modification, or curtailment with the abundance of *T. squamosina,* based on the species' distribution in nearshore habitats, documented evidence of the impact of coastal development on giant clam abundance generally, and ongoing regional development goals, we conclude that this threat poses a high risk to *T. squamosina.* In other words, we find that it contributes significantly to the species' long-term extinction risk and is likely to contribute to its shortterm extinction risk in the near future.

Tanmen Destructive Shell Harvesting

Despite a relatively small geographic scope, giant clam shell harvesting in the South China Sea has caused severe destruction of shallow water habitats. In the last decade, the small fishing village of Tanmen in China's Hainan province became a regional epicenter for giant clam shell handicraft and trade (Hongzhou, 2016; Larson, 2016; Lyons *et al.,* 2018). From 2012 to 2015, the number of retailers of giant clam shell handicraft increased from 15 to more than 460, the number of shell carving workshops increased from a dozen to more than 100, and by the end of this period, it was estimated that this industry supported the livelihood of nearly 100,000 Tanmen residents (Hongzhou, 2016; Bale, 2017; Wildlife Justice Commission, 2021).

As the industry grew, many Tanmen fishermen increasingly abandoned the traditional fishing industry and shifted focus to giant clam shells as their primary livelihood. With local stocks of giant clams having been depleted by a long history of overharvesting, many fleets resorted to destructive methods of digging out large portions of coral reef using their boat propellers to access the shells of long-dead clams that had been buried under the reef substrate (Wildlife

Justice Commission, 2021). As reported by V. R. Lee (2016), harvesting boats are anchored with a long rope or chain against which the propeller holds tension as it carves an arc-shaped scar in the reef (see also Wingfield-Hayes, 2015). The majority of this activity has occurred the South China Sea, and an analysis of satellite imagery revealed extensive damage in the Spratly Islands and Paracels, with an estimated 160 km2 of coral reef in these areas completely destroyed by the combination of clam dredging and island-building activities (McManus, 2017).

In response to international pressures and following a 2016 arbitral tribunal ruling that China was aware of and responsible for ''severe harm to the coral reef environment'' in the South China Sea due in part to these activities (Permanent Court of Arbitration, 2016), steps were taken to halt destructive clam shell harvesting operations. China began to enforce anti-corruption measures aimed at undermining demand for the expensive jewelry and statues carved from giant clam shells (Bale, 2017), and in January 2017 the Hainan Province People's Congress passed new regulations that effectively banned the commercial trade of all giant clam species in Hainan (Wildlife Justice Commission, 2021). However, while giant clam shell harvesting operations were found to decline significantly between 2016 and 2018, the Wildlife Justice Commission (2021) reports several lines of evidence to suggest that ''illegal giant clam shell trade persists in China in a covert manner with one clear supply area'' (Hainan Province), and that a new influx of clam harvesting boats have returned since 2018. Thus, while the extensive damage to the habitat in this region would likely take several decades or more to undo if the ecosystems were allowed to recover, the ongoing threat of illegal harvesting is likely to prevent any substantial habitat recovery in the foreseeable future.

This threat of habitat loss is relevant to the species that are known to occur in this region and that are typically found in reef flat environments where the harvesting operations primarily occur. This includes *T. gigas, T. squamosa, H. hippopus,* and most critically *H. porcellanus,* which has a highly restricted range centered in the Sulawesi region of Indonesia but that extends northward into the Philippines and portions of the South China Sea (Wells, 1997; bin Othman *et al.,* 2010; Neo *et al.,* 2017). As is mentioned above, the damage from these operations has likely eliminated any *H. porcellanus* that may have previously occurred in the islands of the South China Sea.

Overutilization for Commercial, Recreational, Scientific, or Educational Purposes

The pervasive harvest of giant clams for subsistence and domestic sale, and several periods of short-lived but intensive commercial harvest have severely depleted giant clam populations throughout their respective ranges. Once the center of giant clam diversity in the region, the Philippines saw commercial exploitation of giant clams for the international shell trade decimate populations of *H. hippopus, H. porcellanus, T. gigas,* and *T. squamosa.* Similar trends have been observed throughout Southeast Asia (*i.e.,* Indonesia, Singapore, Thailand, Cambodia, Vietnam, and in the South China Sea), where each of these species except *T. squamosa* is now considered rare or locally extinct (Neo *et al.,* 2017). Likewise, illegal harvest of giant clams for the international clam meat trade, primarily by Taiwanese fishermen or to supply Taiwanese demand, severely reduced giant clam populations throughout the western and central Pacific. As a result, as in Southeast Asia, nearly all of the species (excluding *T. squamosa*) are now considered rare or extinct throughout most of their Pacific range (Wells, 1997; Neo *et al.,* 2017). Although international demand (primarily for the aquarium trade) is increasingly met by the growing field of giant clam mariculture, wild-sourced clams are still observed in international trade, and the potential for laundering wild clams with mariculture-produced specimens cannot be discounted (Sant, 1995).

Ongoing harvest for subsistence or domestic market supply, as well as persistent poaching, continues to limit substantial population recovery of giant clams throughout much of their range. As broadcast-spawning organisms with little to no mobility, giant clams are reliant on sufficient population density to facilitate gamete fertilization. Thus, even if small populations of giant clams have survived the years of exploitation, in many cases individuals may be too dispersed to successfully reproduce. Furthermore, the largest individuals were often targeted for the meat and shell trade, leading to altered size structures in remnant giant clam populations. Juveniles and smaller adults are known to be more susceptible to predators and to exhibit lower reproductive output, which will likely continue to limit population recovery in the near future. It is for these reasons that we consider overutilization to be the most significant threat to all seven giant clam species. Below, we

summarize the threats posed by overutilization related to subsistence fisheries, domestic markets, international trade, and illegal poaching, highlighting specific details related to each affected species.

Subsistence Fisheries

Giant clams have long been, and continue to be, an important component of traditional livelihoods and culture throughout their geographic range (Craig *et al.,* 2011). As described by Lindsay *et al.* (2004), ''there are few locations within the Pacific where tridacnids are not gathered on a daily basis and found in local markets'' (Munro, 1993a). Archaeological evidence from shell middens (piles of discarded shells), which can be found across the Indo-Pacific from as far back as 2000 years ago (Swadling, 1977), as well as anecdotal accounts and local fishing practices all point to the importance of giant clam in Indo-Pacific diets (Neo & Loh, 2014). The shells of giant clams are also frequently carved for use as tools, containers, and ornaments (Copland & Lucas, 1988; Lucas, 1994).

Because *H. hippopus* is unattached to the substrate and occupies nearshore habitats that are relatively accessible to humans, it is an easy target for reef gleaners (*i.e.,* fishers that collect organisms by hand from nearshore sand and reef flats). Consequently, it has been a popular species for local harvest and consumption throughout its range. Many years of subsistence harvest have driven widespread population declines and local extirpations from many Pacific island nations and territories, including American Samoa, CNMI, and Guam.

In Fiji, for example, Seeto *et al.* (2012) discovered *H. hippopus* fossils in shell middens from two Lapita-era settlements (1100–550 B.C.), and found that shell size increased with midden depth, suggesting that human consumption contributed to population reductions and to its eventual extirpation. Surveys from Palau in the 1970s indicated that *H. hippopus* populations declined drastically as a direct result of overharvest (Bryan & McConnell, 1975). In Singapore, *H. hippopus* was considered rare historically (S. K. Lee, 1966; Dawson & Philipson, 1989), but consistent harvest pressure is thought to have prevented the species from establishing a sustainable population in the area and ultimately led to its extirpation (Neo & Todd, 2012). Additionally, *H. hippopus* continues to be exploited for consumption by coastal communities in Indonesia (Naguit *et al.,* 2012), Malaysia (Neo & Todd, 2012), New Caledonia (Purcell *et al.,* 2020), the Andaman and

Nicobar Islands (Nandan *et al.,* 2016), Papua New Guinea (Kinch, 2003), and virtually every other country where it occurs, except for Australia (Wells, 1997).

H. hippopus has also been extirpated from American Samoa, CNMI, and Guam due to a long history of harvest for subsistence consumption and for sale in local markets (Munro and Heslinga, 1983; Sant, 1995; Wells, 1997; Green and Craig, 1999; Pinca *et al.,* 2010). According to Score (2017), giant clams have a ''special significance'' in American Samoa culture and are often used as offerings during family and community gatherings when available. Moreover, Cunningham (1992) describes the cultural significance of giant clams to the Chamorro people, who live throughout the Mariana Islands, including CNMI and Guam. The common use of *H. hippopus* as a source of food and to make tools likely led to its extirpation in these locations (Wells, 1997).

Similar to *H. hippopus,* the tendency of *H. porcellanus* to occupy shallow nearshore areas make the species highly vulnerable to harvesting (Dolorosa *et al.,* 2014). Heavy exploitation from both subsistence and commercial harvest has led to severe population declines throughout its range (Dolorosa *et al.,* 2014; Neo *et al.,* 2017). Villanoy *et al.* (1988) determined that *H. porcellanus* was overexploited in the Philippines as early as the 1980s, and more recently, Rubec *et al.* (2001) reported that *H. porcellanus* has been depleted to such an extent that it is no longer commercially viable for harvest in the Philippines. Ultimately, while subsistence harvest was widespread, heavy fishing pressure on giant clam stocks in the Philippines for the commercial shell trade has been the primary cause of population decline, and has led to local extinctions throughout the region (see International Trade in Giant Clam Shells and Shell-Craft below).

Because of their large size and fast growth rates, *T. derasa* and *T. gigas* have historically been two of the most widely exploited giant clam species for the consumption of their meat. Reports from throughout their ranges indicate that both species are harvested for subsistence consumption in nearly every location where they occur, with the major exception being the Great Barrier Reef and northwestern (NW) islands of Australia. There are certain Pacific island communities that attribute unique significance to *T. gigas* as a cultural symbol and place high value on the species as a food item for special occasions (Hviding, 1993). The

shell of *T. gigas* is also valued as a traditional resource among many coastal communities for use as basins or as personal or religious decorations (Juinio *et al.,* 1987; Hviding, 1993; Lucas, 1994). Both *T. derasa* and *T. gigas* are reported to have been extirpated from CNMI and Guam as a result of longstanding subsistence harvest (Wells, 1997; Pinca *et al.,* 2010).

Based on the best available scientific and commercial data, it is likely that past and current subsistence harvest has played a significant role in the low abundance of *T. mbalavuana* throughout its range. S. Lee *et al.* (2018) attributes its absence from areas outside of the eastern Lau group in Fiji to a combination of ecological factors and ''serial overfishing.'' Additionally, Lewis and Ledua (1988) reported that in Fiji, *T. mbalavuana* is occasionally harvested unintentionally with *T. derasa,* due to the similarity in appearance between the two species. In Tonga, *T. mbalavuana* has traditionally been harvested for subsistence consumption and to supply domestic markets (Ledua *et al.,* 1993), and although its occurrence in deeper areas may have offered some protection from harvest historically, the advancement of SCUBA and hookah gear has facilitated greater access to previously inaccessible stocks (Lewis & Ledua, 1988; Lucas *et al.,* 1991; Neo *et al.,* 2017). Interviews with a number of traditional fishermen indicated that the abundance of *T. mbalavuana* in Tonga had declined considerably during their lifetimes (Ledua *et al.,* 1993). Harvest of giant clams for subsistence consumption and domestic markets is ongoing and largely unregulated in Fiji and Tonga.

Compared to the more common *T. maxima* and *T. crocea* (that are not themselves subject to this rulemaking), which often co-occur with *T. squamosa, T. squamosa* is typically larger and easier to physically remove from the reef, which makes it highly susceptible to harvest, particularly in shallow nearshore areas. For this reason, *T. squamosa* is an important resource in subsistence fisheries in nearly every location across its range, and in several locations, it is the preferred giant clam species for meat consumption (Neo *et al.,* 2017). Few exceptions include Australia, where giant clam harvest is strictly prohibited, and remote areas where the distance from human settlements and infrastructure limits accessibility. However, in most locations where the species occurs, longstanding subsistence harvest has reportedly driven widespread population declines (Neo *et al.,* 2017).

There are several studies that provide some insight as to the impact of past and current harvest on the abundance of the *T. squamosina* in the Red Sea. Paleolithic artifacts indicate that modern humans have been exploiting mollusks in the Red Sea for at least 125,000 years (Richter *et al.,* 2008). During this time, Richter *et al.* (2008) found that giant clam communities in the Red Sea have changed dramatically from before the last interglacial period (122,000 to 125,000 years ago), when *T. squamosina* constituted approximately 80 percent of the shell remains, to *T. squamosina* comprising less than 5 percent of shells in freshly discarded shell middens. While the authors acknowledge that variable recruitment rates and mortality among the three Red Sea giant clam species may be attributed to natural disturbances, a concurrent decline in the size of giant clam shells strongly suggests that overutilization has played a significant role (Richter *et al.,* 2008). In general, giant clam stocks in the Red Sea (including *T. maxima, T. squamosa,* and *T. squamosina*) have declined to less than 5 percent of their historical abundance in the 1980s and 1990s, largely due to artisanal reef-top gathering for meat and shells (Richter *et al.,* 2008).

As with *H. hippopus* and *H. porcellanus,* the distribution of *T. squamosina* in shallow, nearshore habitats makes it particularly accessible to reef-top gatherers and exacerbates the threat of overutilization. Bodoy (1984) reported that giant clams had been subject to ''heavy exploitation in the vicinity of Jeddah, Saudi Arabia, and they [were] often collected on the reef flat, both for food and for decorative purposes.'' Additionally, two firsthand accounts from Gladstone (2000, 2002) described the harvest of ''a significant number of clams'' (primarily *T. maxima,* which is not subject to this rulemaking) from the Kharij As Sailah and Kharij Al Qabr areas of the Farasan Islands, noting that ''clams were easily harvested in the shallow reef flats.'' Overall, the best available scientific and commercial data suggest that giant clams have been harvested extensively in the Red Sea for many years, and given their traditional importance in the diets of coastal communities, harvest is likely ongoing in most areas of the Red Sea.

Domestic Markets (Meat and Shells)

In areas where giant clams were historically abundant, commercial fisheries often developed alongside subsistence harvesting to supply the local demand for giant clam meat and shells. In Fiji, *T. squamosa* and *T.*

derasa were harvested by small-scale commercial operations and sold in 11 municipal markets or other direct sales outlets (Lewis *et al.,* 1988). From 1979– 1987, annual sale of giant clam meat in the domestic market ranged between 6 and 42 tons (Adams, 1988; Lewis *et al.,* 1988; Wells, 1997). With respect to both species, Lewis *et al.* (1988) reported that the commercial harvest had driven once abundant populations to low densities, particularly near major urban centers.

Local markets also exist in a number of other Pacific countries and territories, although data on giant clam meat are often not reported at the species level. This is because of the difficulty in identifying the species once the meat is harvested since the shells are often left in the water, or because giant clam meat may have been mixed together or recorded collectively with other shellfish products when it was landed. Wells (1997) reported varying prices for giant clam meat from markets in American Samoa, the Solomon Islands (amounting to about 1 tonne of giant clam meat sold per year), the Marshall Islands (*H. hippopus* and *T. squamosa*), Niue, Vanuatu, Samoa, and FSM, where in 1990, 3.66 tonnes of giant clam meat were sold in the main markets of Chuuk. Data collected over a 10-week period in Tonga suggested that annual landings of giant clam meat for the domestic market might be 639–1,346 kg (Tacconi & Tisdell, 1992). Wells (1997) noted that in Jepara, Indonesia, giant clam meat was often sold dried, suggesting that the lack of fresh meat may be due to local overutilization of stocks. In Myanmar, clam meat was often marketed fresh for local consumption (Munro, 1989).

Additional reports indicate that domestic markets have continued in many of these localities into at least the early 2000s. In 1998–1999, nearly six tonnes of giant clam products were sold at a single market in Samoa (Skelton *et al.,* 2000). Giant clam meat was still reported to be sold openly at markets in Malaysia as of 2003 (Shau-Hwai & Yasin, 2003). Until bag limits were established in 2009, the declared commercial catch of giant clams in New Caledonia varied between 1.5 and 9 tonnes per year. This included *T. derasa, T. squamosa,* and *H. hippopus,* and the authors indicate that it is often the adductor muscle that is sold in stalls of local markets. In the decade since the bag limits were put in place, commercial catch has fallen below 2 tonnes per year (Purcell *et al.,* 2020). Kinch and Teitelbaum (2010) report that a high demand for giant clams to supply the local market in Tonga ''has resulted in the over-exploitation of giant clam stocks in some areas.'' In Papua New

Guinea, Kinch (2003) attributes sparse populations of giant clams to commercial harvest, particularly that of Brooker Islanders. From January to September 1999, the author recorded the total sales of giant clam adductor muscle from Brooker Islanders to a local fishing company, which included 551 kg (or 1,970 clams) of specimens under 400 g and 146 kg (or 170 clams) greater than 400 g. Notably, nearly one-third of the *T. gigas* individuals included in these sales were not full-grown adults, which likely had an effect on the future productivity of those populations. Similarly, harvesting of giant clams for sale and subsistence use in Vanuatu has led to severely reduced populations that are ''now considered close to collapse in many locations despite the presence of suitable habitats for juveniles and adults'' (Dumas *et al.,* 2012).

Domestic markets for giant clam shells are often related to the tourism industry. In the Andaman and Nicobar Islands of India, Nandan *et al.* (2016) report that giant clams, including *T. squamosa* and *H. hippopus,* are fished for the tourism-based ornamental shell industry. Additionally, in Thailand, giant clams shells are usually first sold to local traders in Phuket, and then sold to tourists as ornamental shells or various shell crafts (*e.g.,* ashtrays, soap trays, lamps) (Chantrapornsyl *et al.,* 1996). Shells have also been a popular souvenir for tourists visiting beach and resort areas of the Philippines and Indonesia (Tisdell, 1994). At the Pangandarin and Pasir Putah beach resorts in Java, Indonesia, as many as 39 and 35 giant clam shells, respectively, were available for sale in 2013, despite a prohibition on the harvest and sale of giant clams (except under ''exceptional circumstances'') under Indonesian law since 1987 (Nijman *et al.,* 2015).

Prior to this prohibition, a major industry based on the use of giant clam shells for production of floor tiles (a.k.a, 'teraso' tiles) led to the extensive harvest of giant clams in Indonesian waters. While much of the shell material was dead shells of *T. derasa* and *T. gigas* buried in reef flats, living specimens were known to be taken when found (Lucas, 1994). As described by Lucas (1994), there were tile production centers at Jakarta, Semarang, Bali, Manado, and likely Suabaya in the early 1980s, and clam shell trade routes had developed throughout the Indonesian islands to supply the industry. The best estimates of giant clam shell import to the Semarang tile production center from the nearby Karimun Jawa islands varied between about 20 and 200 tonnes per month over the period 1978–1983 (Brown & Muskanofola, 1985). At the

Jakarta production center, the clam shell trade was estimated to reach at least 600 tonnes per month in 1982 (Usher, 1984 cited in Lucas, 1994). This industry is no longer active in Indonesia as a result of the 1987 prohibition; however, it is likely that such intense demand contributed significantly to the depletion and current rarity of *T. derasa* and *T. gigas* in Indonesian waters and limited any potential for their recovery. Moreover, despite regulatory protection, all species of giant clams remain heavily exploited in Indonesia for their meat and shells, and some for the live aquarium trade (Neo *et al.,* 2017). As a result of this overutilization, the larger giant clam species are now thought to occur in only a few locations archipelago-wide (Hernawan, 2010).

International Trade of Giant Clam Meat and Poaching

While giant clam meat is consumed throughout the Indo-Pacific region, Taiwan has consistently had the largest market and demand for giant clams. Some of the earliest references indicate that giant clams around Taiwan were depleted many decades ago (Pearson, 1977; Tisdell & Chen, 1994). As local stocks were rapidly exhausted, Taiwanese vessels began to range farther from their home ports, and from the 1960s to the mid-1980s, a surge of Taiwanese fishing vessels began illegally entering the waters of other Pacific nations in search of giant clam adductor muscle, particularly from the larger species, *T. gigas* and *T. derasa* (Munro, 1993a; Kinch & Teitelbaum, 2010). Occasionally, these vessels operated under agreements with local communities in exchange for resources (Adams, 1988), but in the vast majority of cases, giant clams were harvested illegally and to an unsustainable degree (Lucas, 1994; Kinch, 2002). The clam poachers progressively worked their way through the Pacific, typically concentrating their efforts on uninhabited islands and reefs where giant clam stocks had been virtually untouched and where local surveillance was limited. Reports of Taiwanese poaching include areas of the Philippines, FSM, Indonesia, Papua New Guinea, the Solomon Islands, Australia (the Great Barrier Reef), Palau, Fiji, Kiribati, and the Marshall Islands (Dawson & Philipson, 1989; Sant, 1995).

Data on the landings of giant clam meat in Taiwan are generally unavailable due both to their illegal nature and because in the records, landings were combined with meat of other marine molluscs and collectively referred to as 'ganbei' or 'compoy' (Lucas, 1994; Tisdell & Chen, 1994).

Tisdell and Chen (1994) report that imports of ganbei ranged from 9 tons in 1977 to 621 tons in 1988. Other estimates of giant clam adductor muscle landings in the 1960s and 1970s range between 100 and 400 tons per year (Carlton, 1984; Dawson & Philipson, 1989). Dawson and Philipson (1989) estimated that during the peak of the Taiwanese fishery for giant clams, harvest did not likely exceed 100 tons of adductor muscle per year, though Munro (1989) regarded this to be an underestimate. Accounting for the potential harvest of the smaller species, *T. derasa* and *H. hippopus,* which have an adductor muscle about one-third the weight of *T. gigas,* those landings correspond to 300,000 to 450,000 clams per year. According to Dawson (1986), ''it seems certain [. . .] that the total illegal harvest of giant clams over the twenty-odd years that such activities have occurred in the region can safely be measured in the millions.''

Poaching by long-range Taiwanese vessels peaked in the mid-1970s and gradually declined during the 1980s as the extension of exclusive economic zones, improved surveillance of reef areas, boat seizures, and depleted stocks made the fishery less profitable (Lucas, 1994). In addition, growing pressure from many Indo-Pacific nations forced the Taiwanese government to take stricter actions against giant clam harvesters (Dawson, 1986). The last five 'compoy' (*i.e.,* clam and other shellfish) fishing licenses were rescinded by the Taiwanese government in 1982, mainly due to pressure from the Australian government, and beginning in 1986, the Taiwanese government began rejecting all requests for approval of Taiwanese involvement in any clam fishing activities, regardless of whether foreign agreement or license documents were provided. There is evidence, however, that some poaching activities continued in remote locations. From 1982 to 1987, at least four Taiwanese vessels were apprehended on outlying reefs of the Solomon Islands, in each case carrying clam meat from tens of thousands of giant clams (Govan *et al.,* 1988). The authors note that the small size of the adductor muscles recovered indicates that large clams had likely already been harvested from the reef at an earlier date.

Even as Taiwanese poaching operations declined, the demand for giant clam meat in Taiwan persisted, incentivizing the development of legal commercial fisheries for export throughout the Indo-Pacific (Lewis *et al.,* 1988; Basker, 1991; Lucas, 1994). It was estimated that imports of adductor muscle to Taiwan from these newly

formed fisheries totaled approximately 30–40 tons in 1987 and 1988 (Tisdell & Chen, 1994). The fisheries, however, rapidly depleted local stocks and were in most cases short-lived, typically being shut down by local authorities in the span of a few years. In the Maldives, for example, commercial harvest of giant clams began in June 1990 and continued until early in 1991. Two buyers were operating and collectively harvested over 90,000 individuals; one buyer exported 9.8 tons to a Taiwanese buyer (Basker, 1991). Concerned over the high exploitation rate, the Ministry of Fisheries and Agriculture conducted an assessment of the giant clam stocks and fishery, and the resulting report recommended closing off high density areas to further fishing and other restrictions (Basker, 1991). The commercial fishery was subsequently closed, and collection of giant clams remains prohibited in the Maldives. Likewise, a commercial fishery in Papua New Guinea reportedly removed at least 85 tons of adductor muscle over a 5-year period, equivalent to over 750 tons total flesh weight, until it was closed due to depleted stocks (Munro, 1993a).

Adams (1988) described one example of the impact of extreme commercial harvesting pressure in Fiji when a ship named 'Vaea' intensively harvested giant clam stocks in 1985. Teams of two harvesters on Hookah gear reportedly caught 50–250 clams per day. At one site, harvesters had taken approximately 80 percent of the standing stock of *T. derasa,* or nearly 15,000 individuals, from an area of 25.9 square miles down to a depth of 20 meters. Adams (1988) estimated that harvesting rates averaged 70 percent of the total living stock at each reef, less for scattered populations and more for denser ones. From 1984 to 1987, *T. derasa* catch rates in Fiji varied between 20 and 40 tons of flesh per year, half of which was exported (Adams, 1988). The Fijian fishery as a whole (including municipal markets, wholesale and retail outlets, and exports) landed over 149 tons during this period, with the largest annual harvest reaching 49.5 tons in 1984, the year in which exports began (Lewis *et al.,* 1988).

By the early 1990s, pervasive stock depletions across the Indo-Pacific severely limited Taiwanese imports of giant clam meat (Tisdell and Chen, 1994). In the years since, many countries in the region have banned commercial export of giant clams, some have imposed size and/or bag limits, and many have become signatories to the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES). The regulatory

implications of CITES participation are discussed more thoroughly below in the section on *Inadequacy of Existing Regulatory Mechanisms,* but one of its requirements is that Parties must submit an annual report of their trade in CITESlisted species, including the number and type of permits and certificates granted, the countries involved, and the quantities and types of specimens traded. All species of giant clams have been listed under appendix II of CITES since 1985, and we can therefore rely to some extent on trade statistics from the CITES reporting database to characterize more recent patterns in the international market for giant clams.

In most cases, countries have limited their reporting to the family or genus level, and outside of a few instances of trade reported for *T. derasa, T. gigas,* and *T. squamosa,* no other species were identified specifically. Additionally, of all the transactions reported from 1983 to 2020, 50.4 percent and 39.5 percent were en route to New Zealand and the United States, respectively, while Japan, Singapore, and Australia comprised the remaining 10.1 percent of imports. Law Enforcement Management Information System (LEMIS) trade data provided by USFWS for the period 2016–2020 indicate that nearly all of the imports of giant clam meat over the past 5 years were classified to be of 'Personal' nature, likely representing shipments intended for families or friends of Pacific islanders (Shang *et al.,* 1994). Prior to 2000, there are several years in which countries reported significant export of meat from giant clams that had been born or bred in captivity. This includes 3615 kg and 472 kg of *T. gigas* and *T. derasa* meat, respectively, exported from Solomon Islands in the 1990s, 1695 kg of *T. derasa* meat exported from Palau in 1990–1991, and 65 kg of *T. gigas* meat exported from Australia.

A number of other countries have reported significant export of giant clam meat (species unknown) since the late 1990s, primarily to New Zealand and the United States. Nearly all of these exports are of wild-caught specimens, many of which have been seized or confiscated at the border due to improper or missing CITES export permits. The major exporters of giant clam meat in the last two decades include the Cook Islands, Kiribati, Marshall Islands, FSM, and Tonga. At the higher end, Tonga has exported an average of 1210 kg giant clam meat per year since 2005, and at the lower end, the FSM has averaged 58 kg per year during the same period.

Importantly, a number of the key countries in the trade of giant clam meat

are not CITES contracting parties (*e.g.,* Cook Islands, Kiribati, Marshall Islands, FSM) or have only become so relatively recently (*e.g.,* Palau in 2004, Solomon Islands in 2007, Tonga in 2016). Thus, any trade reported for these countries is based on values reported by the CITES party involved, and any trade among two non-contracting nations is not included in these estimates. Additionally, the USFWS Office of Law Enforcement in Honolulu, Hawaii has reported that approximately 450 lbs (200 kg) of giant clam meat per year is refused (*i.e.,* seized, confiscated, or reexported) from Tonga, FSM, and the Marshall Islands (K. Swindle, USFWS, pers. comm., December, 2017). This is likely a significant underestimate of the total amount of giant clam meat that comes into the United States (as a whole) illegally, as many shipments outside of those that pass through Honolulu likely make it past enforcement inadvertently (K. Swindle, USFWS, pers. comm., December, 2017). For these reasons, the CITES data should be viewed as incomplete, and the reported quantities are likely an underestimate of the total trade in giant clam meat.

International Trade in Giant Clam Shells and Shell-Craft

Giant clam shells have been used for a variety of decorative and utilitarian purposes, including as beads, vases, lamps, ashtrays, and wash basins. *H. hippopus* and *T. squamosa* are considered the most popular giant clam species for the shell trade (Shang *et al.,* 1994) because of their unique physical characteristics (*e.g.,* attractive colors, bowl-like shape, *etc.*), although nearly all of the species have been harvested depending on the intended use, cultural preference, or geographic availability.

The Philippines has historically operated as the largest exporter of giant clam shells and shell-craft, accounting for over 95 percent of the global exports of giant clam shell products from 1983 to 2020. During the peak of the shell trade from 1979 to 1992, total exports from the Philippines surpassed 4.2 million kg (Juinio *et al.,* 1987; Wells, 1997). While all species of giant clam that occur in the Philippines have been exploited, the two *Hippopus* spp. and *T. squamosa* were the most frequently used for ornamental purposes and handicrafts, and *T. gigas* was most frequently used for basins (Lucas, 1994). Juinio *et al.* (1987) noted that *T. derasa* may have also been harvested but was often not distinguished by shell dealers as a separate species; rather, it was known as a ''heavier variety'' of *T. gigas* or *H. porcellanus.*

Export records from the Philippines Bureau of Fisheries and Aquatic Resources indicate an initial peak in 1979, when 1,003 tonnes of giant clam shells were exported, corresponding to 895,000 shell pairs. Exports then declined to a minimum of 63 tonnes (or 67,000 shell pairs) in 1982, which was thought to reflect saturation of the international demand. Juinio *et al.* (1987) reported that the demand for giant clam shells could be met from existing stock piles (except those of *H. porcellanus,* which was still considered to be highly marketable). However, exports began to increase again in the late 1980s and peaked in 1991 with nearly 1.2 million shells, over 460,000 carvings, and over 1,186 tonnes of shells (equivalent to about 825,000 shell pairs) exported in a single year (Wells, 1997). This occurred despite the government of the Philippines instituting a ban on the export of giant clams (except *T. crocea,* not subject to this rulemaking) in 1990. In the following year, exports declined to 374,000 shells and 70,000 carvings, likely due to the issuance of CITES Notification No. 663 (16 January 1992) urging all CITES Parties to refuse trade permits for Tridacninae products from the Philippines, in accordance with Philippine legislation (Wells, 1997). In the three decades since 1992, reported exports of giant clam shells from the Philippines have been considerably lower (but not absent), totaling only 8,528 shells and 6,359 carvings (CITES Trade Database, accessed 22 Mar 2022).

Ultimately, widespread subsistence harvest in conjunction with the heavy fishing pressure on giant clams to supply the commercial shell trade decimated the populations of several giant clam species (*e.g., H. hippopus, H. porcellanus, T. gigas,* and *T. squamosa*), with local extinctions widespread throughout the Philippines (Juinio *et al.,* 1987). Wells (1997) reported that exports until 1992 were dominated by *H. hippopus, T. squamosa,* and *H. porcellanus,* with *H. hippopus* comprising 53 percent of shell exports and 94 percent of carvings. Even the few remaining locations thought to be the species' last strongholds in Philippine waters (*e.g.,* in the Sulu Archipelago and Southern Palawan) were overharvested by the mid-1980s (Villanoy *et al.,* 1988). Presently, five of the seven giant species considered here (*H. hippopus, H. porcellanus, T. derasa, T. gigas,* and *T. squamosa*) can still be found in the Philippines and they are all protected by Philippine law. Native *T. gigas* populations are restricted to small portions of Tubbataha Reefs Natural Park in very low abundances; *T. derasa,*

H. hippopus, and *H. porcellanus* are considered rare, and *T. squamosa* is considered frequent (Neo *et al.,* 2017).

The United States, Japan, Australia and various European countries have historically been the largest importers of shells and shell-craft from the Philippines (Juinio *et al.,* 1987; Wells, 1997). The United States alone has accounted for over 50 percent of shells and over 60 percent of shell carvings imported between 1983 and 2020. More recently, however, dwindling giant clam populations as well as greater regulatory protections in many countries have limited the shell trade among the traditional major importers of the 1980s. Instead, the majority of international trade has shifted increasingly to illegal means. From 2016 to 2020, the global trade in giant clam shells based on CITES reports totaled 65,129 shells and 221 shells carvings (primarily *T. gigas*), of which over 92 percent originated in Indonesia and over 97 percent was imported by China. This has occurred despite a prohibition on the harvest and export of giant clams under Indonesian law since 1987. While not at the same scale as the Philippines, Indonesia has participated in the trade of giant clam shells and shell products since the 1980s. Once giant clams were listed as protected species in 1987, Tisdell (1992) suggested that unrecorded exports of giant clam shells continued to occur from Indonesia to the Philippines. Likewise, several reports in the years since indicate that enforcement of the harvest and export ban remains grossly insufficient and, as is suggested by the CITES reports, substantial export of giant clam shells from Indonesia is ongoing (Allen & McKenna, 2001; Nijman *et al.,* 2015; Harahap *et al.,* 2018).

Presently, the largest market for giant clam shells is in the city of Tanmen, in the southern Chinese Province of Hainan. As discussed previously, a major shell-crafting industry developed in this region during the 2000s. During the peak of the Tanmen shell-crafting industry in 2013–2014, there were an estimated 150 processing workshops supplying 900 craft shops with giant clam shell products in the province (Wildlife Justice Commission, 2021). The annual sales revenue of giant clam shell handicrafts in 2014 was estimated to be \$75 million USD (Lyons *et al.,* 2018). In January 2017, the Hainan Province People's Congress passed new regulations banning the commercial trade of giant clams in Hainan. However, investigations conducted 2 years later by the Wildlife Justice Commission (2021) found that there were still more than 100 craft shops in

Tanmen, although fewer than 20 percent were still in business. Giant clam shell products were also being sold openly in hundreds of stores in other parts of the Hainan Province, such as Haikou, Sanya, Guangdong and Fujian provinces, and could be ordered on social media platforms, such as WeChat, for delivery to other locations (Wildlife Justice Commission, 2021). This has been corroborated by first-hand news reporting from Scarborough Shoal in April 2019, which documented ongoing shell harvesting by fishing boats flying the Chinese flag (ABS–CBN News, 2019). The ABS–CBN film crew captured many large piles of extracted giant clam shells around the harvesting area, some even extending above the water surface.

This industry primarily targets the shells of deceased clams embedded in the reef substrate; however, live clams are also taken whenever found. Large shells in particular are of the highest value, putting the remaining *T. gigas* populations in the area at the greatest risk. According to Lyons *et al.* (2018), ''the more valuable [*T. gigas*] pieces come with a certificate of origin, specifying, for example, that it comes from Scarborough Shoal, Spratlys, or Paracels and, occasionally, even the specific reef concerned.'' This suggests that *T. gigas* shells are considered to have different grades or qualities depending on where in the South China Sea they were harvested. As a result of this intense market demand in combination with the destructive shell harvesting methods described above, Gomez (2015) noted that *T. gigas* is now ''virtually extinct'' in the center of the South China Sea, including the Paracels, the Macclesfield Banks, and the Spratlys.

International Trade of Live Giant Clams for Aquaria

The largest current market for giant clams is that of live specimens for the aquarium trade and, to a lesser extent, to supply broodstock for mariculture operations. It can be difficult to distinguish the purpose of live specimen transactions from CITES reports alone, but Wells (1997) concluded ''that the aquarium trade is now the main market for both wildcollected and mariculture clams.'' In the 25 years since that report, the market for giant clams as aquarium specimens has continued to grow, with giant clams now representing one of the most desired groups of invertebrates in the aquarium industry (Wabnitz *et al.,* 2003; Teitelbaum & Friedman, 2008; Mies, Dor, *et al.,* 2017). They are a sought-after commodity and have been described as

a ''must have'' item by collectors and aquarium hobbyists (Lindsay *et al.,* 2004). The smaller, more brightly colored species (*i.e., T. maxima* and *T. crocea,* species not subject to this rulemaking) are by far the most popular in the marine ornamental trade, but *T. squamosa, T. gigas, T. derasa,* and *H. hippopus* are also traded in smaller numbers (Lindsay *et al.,* 2004; Kinch & Teitelbaum, 2010).

CITES records indicate that the primary source countries for the seven species considered here include Australia, Palau, Vietnam, Solomon Islands, and Marshall Islands, among others. Notably, the vast majority of giant clams exported from Australia, Palau and Marshall Islands have been bred/born in captivity and thus pose less risk to wild populations; however, much of the export volume from Vietnam, Solomon Islands, Tonga, and more recently, Cambodia, are of wildsourced specimens.

Of the seven species considered here, *T. derasa* and *T. squamosa* have been the most popular in the trade of live specimens, according to CITES reports. Comparing the two, exports of *T. derasa* have been higher from Pacific island nations, such as Palau, Solomon Islands, Marshall Islands, Tonga, and FSM. Nearly all recent trade of this species is of captive-bred/born individuals, with wild harvest in these countries contributing minimally, if at all, by 2010. *T. squamosa,* by comparison, has been harvested more often by countries in Southeast Asia, such as Vietnam, Cambodia and Indonesia, and many of the recent exports from Vietnam and Cambodia are of wild-sourced individuals. Exports from Vietnam peaked in the 2000s and have declined over the last decade, while exports from Cambodia have increased more recently, reaching nearly 10,000 *T. squamosa* specimens in 2019. Neo *et al.* (2017) notes that the decline in exports from Vietnam is related to trade restrictions implemented in response to concerns and regulations sourcing wild specimens, and it is possible that some giant clams from Vietnam have been rerouted for export through Cambodia. In fact, according to CITES reports, over 99 percent of the recorded *T. squamosa* exports from Cambodia were imported by Vietnam, implying a close trade connection between the two nations. Neither *H. hippopus* nor *T. gigas* have been harvested consistently for the aquarium trade, although with respect to *T. gigas,* Craig *et al.* (2011) attributed this to a lack of available supply rather than a decline in demand. Because of declining populations throughout much of its range, the majority *T. gigas*

specimens for the aquarium trade in the late 2000s were being sourced from just a few small island nations, primarily Tonga (Craig *et al.,* 2011). However, according to CITES records, trade of *T. gigas* from Tonga has not occurred since 2011. *T. gigas* is not considered to be native to Tonga, but had reportedly been introduced there as part of stock enhancement and aquaculture programs (Munro, 1993a; Wells, 1997). According to a CITES assessment in 2004, the introduced populations of *T. gigas* had by that point died out, so it is not clear where the exported specimens originated (CITES, 2004a).

The United States has consistently been one of the top import markets for live giant clams, along with Canada, several countries in Europe, Japan and Hong Kong (Wabnitz *et al.,* 2003; Craig *et al.,* 2011). In 2002, 70 percent of the giant clams exported for the aquarium trade went to the United States (Mingoa-Licuanan & Gomez, 2002 cited in Craig *et al.,* 2011). According to CITES reports from 1983–2020, the United States has accounted for 24.2 percent of the total recorded imports of *H. hippopus,* 53 percent of imports of *T. derasa,* 56 percent of imports of *T. gigas,* 38.4 percent of imports of *T. squamosa,* and 12.8 percent of imports of Tridacninae specimens that were not identified to the species level. Throughout the full record since 1983, 50.6 percent of the imports to the United States were recorded as captive-bred/born specimens, while 44.7 percent were recorded as wild-sourced; however, according to LEMIS data for the period 2016–2020, wild-sourced specimens now represent only 4 percent of imports, with captive-bred/born specimens accounting for the remaining 96 percent.

Summary of Risks to Specific Species Due to Overutilization for Commercial Purposes

After considering the best available scientific and commercial data presented above and in the Status Review Report, we reached several different conclusions regarding the threat of overutilization for various commercial purposes to the seven giant clam species considered here. We summarize these conclusions of the risks for this threat category for each species below.

H. hippopus

A long history of subsistence harvest punctuated by two decades of intense commercial exploitation for the shell and shell-craft industry have led to severe declines of *H. hippopus* populations throughout its range. As is

mentioned above, *H. hippopus* has been one of the most popular giant clam species in the international shell trade because of its size and physical characteristics (*e.g.,* attractive colors, bowl-like shape) (Shang *et al.,* 1994). The Philippines operated as the largest exporter of giant clam shells in the 1970s and 1980s, with *H. hippopus* being the most frequently traded species during this time. According to CITES annual report data, over 277,000 kg, 341,000 shell pairs, 2 million ''shells'' (without associated units), and 1.7 million shell carvings of *H. hippopus* were exported from the Philippines from 1985 to 1993. This period of intense harvest left *H. hippopus* severely depleted throughout the Philippines and much of Southeast Asia, where it remains at very low abundance except in a few isolated areas.

While most countries have imposed prohibitions on the commercial exploitation of giant clams and CITES records indicate that recent international trade of *H. hippopus* is minimal, subsistence harvest continues to pose a threat to the species in most populated areas where it occurs. Without more thorough monitoring from many of these locations, it is difficult to determine if this ongoing harvest is causing further population declines, but at the very least, it is likely preventing any substantial rebound of depleted populations throughout its range. An important exception is Australia, where anecdotal reports suggest that strictly enforced harvest bans have been largely successful in preventing overutilization and protecting reportedly healthy stocks of this species. For these reasons, and considering the documented effects of past harvest for the international shell trade on species abundance, we conclude that overutilization of *H. hippopus* contributes significantly to the species' long-term risk of extinction.

H. porcellanus

As is mentioned above, heavy fishing pressure on *H. porcellanus* in the Philippines for the commercial shell trade has been the primary cause of population decline, and has led to local extinction of the species throughout the region (Juinio *et al.,* 1987). Villanoy *et al.* (1988) documented the export volume of giant clam shells from one major shell dealer in the Zamboanga region of the Philippines, San Luis Shell Industries. From 1978 to 1985, approximately 413,230 pairs of shells were exported by this company, of which about 37 percent (or nearly 153,000) were *H. porcellanus.* Based on comparisons to data provided by Juinio

et al. (1987), the authors estimate that this shell dealer accounted for approximately 18.5 percent of the estimated total export volume of giant clam shells from the Zamboanga region during this period, suggesting that the total harvest of *H. porcellanus* during this period was likely much higher. According to CITES annual reports, from 1985 to 1992, the Philippines exported an additional 576,298 *H. porcellanus* shells, 145,926 shell pairs, 179,043.5 kg of shell material, 293,110 shell carvings, and 38,138 kg of shell carvings. All were either reported to be wild-caught or did not include the source of harvest. No other nation reported export volumes close to this magnitude during this time. Malaysia reported the export of 500 kg of shell material in 1985, and Indonesia reported the export of 100 kg of shell material in 1986, but there are no other CITES reports relating to *H. porcellanus* from these two countries. CITES reports also indicate that 16 *H. porcellanus* were exported as live specimens from the Philippines to Norway and Germany in 1992 and 1997, respectively; there have been no exports of live *H. porcellanus* specimens since. Additionally, export of 35 live specimens from the Solomon Islands to Germany and the United States was reported in 1997, but this is likely a reporting error, as this species has not been observed in the Solomon Islands.

In Indonesia, *H. porcellanus* is extremely rare. It was historically, and still is reportedly, exploited for its meat and shells when it is found (Pasaribu, 1988; Neo *et al.,* 2017). Consequently, the species is now thought to occur in only a few locations in Indonesia (Hernawan, 2010; Wakum *et al.,* 2017). Likewise, *H. porcellanus* abundance is also declining in Malaysia, in part due to ongoing harvest of meat and shells (Neo *et al.,* 2017). As they are considered rare and are restricted to Sabah and Pulau Bidong on the east coast of Peninsular Malaysia, continued harvest likely threatens the persistence of these populations. Additionally, international poaching continues to pose a threat, as authorities from both Malaysia and the Philippines reported an increase in the number of fishing boats illegally harvesting giant clams as recently as 2010–2015 (Neo *et al.,* 2017).

Overall, it is clear that intense historical commercial demand for *H. porcellanus* led to severe population declines and the current low abundance of the species throughout its range. Furthermore, ongoing subsistence harvest and poaching of giant clams throughout the South Asia region continue to threaten the few

populations of *H. porcellanus* that remain. Accordingly, we conclude that overutilization is contributing significantly to the long-term extinction risk of *H. porcellanus* and is likely to contribute to short-term extinction risk in the near future.

T. derasa and T. gigas

Due to the similarities of the threat to *T. derasa* and *T. gigas,* we present the conclusions for these two species together. Overall, the best available scientific and commercial data indicate that both *T. derasa* and *T. gigas* have been widely exploited for many years for their meat, shells, and as popular aquarium specimens. Many consider *T. gigas* to be the most heavily exploited among all giant clams (Craig *et al.,* 2011; Mies, Scozzafave, *et al.,* 2017; Neo *et al.,* 2017), noting its extensive harvest for its meat and shells in nearly every location where it has occurred. Similarly, *T. derasa* is also highly valued as a food source throughout the entirety of its range. For over two decades, both species were subject to an intense commercial demand for the meat of their adductor muscle, primarily from consumers in Taiwan. Widespread harvest and poaching to supply this commercial market caused severe, documented population losses throughout the majority of the species' ranges. The commercial demand for giant clam meat began to decline by the end of the 1980s due to the low abundance of remaining populations in conjunction with stricter harvest regulations and improved enforcement. However, due to their traditional importance as a food source in many cultures, subsistence harvest of *T. derasa* and *T. gigas* continues in most locations throughout their respective ranges, which may lead to further population decline and likely prevents any substantial recovery of depleted populations.

Furthermore, recent CITES records and available reports indicate that *T. gigas* shells continue to be traded in high volumes from Indonesia to China despite a prohibition on the harvest and export of giant clams that has been in place under Indonesian law since 1987 (Allen & McKenna, 2001; Nijman *et al.,* 2015; Harahap *et al.,* 2018).

The Great Barrier Reef and outlying islands of NW Australia are, for the most part, an exception to the rangewide trends for these species. Northern areas of the Great Barrier Reef were subjected to widespread poaching of *T. derasa* and *T. gigas* in the 1970s and 1980s, but improved surveillance of Australian fishing grounds and stronger enforcement of harvest bans reduced the

poaching pressure considerably. As a result, harvest of the two species in Australian waters since the 1980s has likely been minimal. Recent quantitative estimates of abundance are scarce, but based on past surveys and the strong protective measures in place, most experts consider the Great Barrier Reef to have relatively large, stable populations of giant clams, including *T. derasa* and *T. gigas* (Neo *et al.,* 2017; Wells, 1997).

Overall, we consider the severe impact of past harvest on species abundance range-wide alongside reports of ongoing subsistence and commercial use in most locations except Australia. Based on this information, we conclude that overutilization of *T. derasa* and *T. gigas* contributes significantly to the species' long-term extinction risk. However, because the threat is minimal in Australia, which represents a substantial proportion of suitable habitat within these species' respective ranges, and where populations are reportedly healthy, this factor likely does not constitute a danger of extinction to the two species in the near future.

T. mbalavuana

As is discussed above, harvest of giant clams for subsistence consumption and domestic markets is ongoing and largely unregulated in Fiji and Tonga. Thus, given the highly restricted range and general scarcity of *T. mbalavuana,* we conclude that the threat of overutilization for commercial purposes contributes significantly to the species' long-term extinction risk and is likely to contribute to the short-term risk of extinction in the near future.

T. squamosa

T. squamosa has been harvested extensively for both subsistence and commercial purposes for several decades, which has led to documented population declines in many areas of its range (Neo *et al.,* 2017). While most countries have imposed prohibitions on the commercial exploitation of giant clams, the demand for *T. squamosa* in the ornamental aquarium market continues to pose a threat to wild populations in Cambodia and Vietnam. Additionally, subsistence harvest is ongoing in most populated areas where the species occurs. Without more thorough monitoring from many of these locations, it is difficult to determine if this ongoing harvest is causing further population declines, but at the very least, it is likely preventing any substantial rebound of depleted populations throughout its range. As with other species, an important

exception is Australia, where anecdotal reports suggest that strictly enforced harvest bans have been largely successful in preventing overutilization and protecting reportedly healthy stocks of giant clams. For these reasons, and considering the documented effects of past harvest on species abundance, we conclude that overutilization of *T. squamosa* contributes significantly to the species' long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future.

T. squamosina

The best available scientific and commercial data suggest that giant clams (including *T. squamosina*) have been harvested extensively in the Red Sea for many years. Given their traditional importance in the diets of coastal communities, harvest is likely ongoing in most areas of the Red Sea. In combination with the natural accessibility of *T. squamosina* in shallow nearshore areas, this past and ongoing harvest pressure has likely contributed significantly to the exceptionally low abundance of this species throughout the region. We are aware of 30 documented observations of *T. squamosina* since its re-discovery in 2008. This includes 17 specimens from the Gulf of Aqaba and northern Red Sea (Roa-Quiaoit, 2005; Richter *et al.,* 2008; Huber & Eschner, 2011; Fauvelot *et al.,* 2020), seven individuals from the Farasan Islands in southern Saudi Arabia (Fauvelot *et al.,* 2020; K.K. Lim *et al.,* 2021), and six individuals from an unnamed site in the southern Red Sea (Rossbach *et al.,* 2021). As an indication of its exceptionally low abundance at present, Rossbach *et al.* (2021) surveyed 58 sites along the entire eastern coast of the Red Sea, from the Gulf of Aqaba down to southern Saudi Arabia, and observed six *T. squamosina* at only one survey site in the southern Red Sea. Similarly, Pappas *et al.* (2017) did not encounter any *T. squamosina* at nine survey sites in the central Red Sea. With so few *T. squamosina* remaining, we conclude that this factor is likely to contribute to short-term extinction risk in the near future.

Disease or Predation

There are a number of infectious diseases and parasites that have been reported in giant clams, most often either bacterial or protozoan in origin (Braley, 1992; Mies, Scozzafave, *et al.,* 2017). Bacterial infections are most often caused by *Rickettsia* sp., which infect the ctenidia (gill-like respiratory organ) and the digestive lining of the clam (Norton *et al.,* 1993; Mies, Scozzafave, *et al.,* 2017). Protozoan

infections are often caused by either *Marteilia* sp. or *Perkinsus* spp. Giant clams with *Marteilia* infections show no external symptoms, but the infection will eventually cause superficial lesions on the kidney (Mies, Scozzafave, *et al.,* 2017).

Perkinosis, also known as pinched mantle syndrome, is caused by *Perkinsus* spp. Giant clams typically do not exhibit any symptoms of the infection until they become immunosuppressed due to some other environmental stress. At that point, the protozoan population is able to proliferate, and in some cases causes mortality of the host clam. Once the clam dies, trophozoites of *Perkinsus* spp. become waterborne and can infect nearby individuals (Mies, Scozzafave, *et al.,* 2017). A significant rate of infection by *Perkinsus* spp. was previously observed at several sites on the Great Barrier Reef, with 38 of 104 sampled individuals (including *T. gigas* and *H. hippopus*) being infected (Goggin & Lester, 1987). Additionally, several *Perkinsus* infections were observed in association with a mass mortality of giant clams at Lizard Island in Australia in 1985; however, the cause of the death was never determined and the infections may have been coincidental (Alder & Braley, 1989).

Giant clams are also affected by external parasites, including snails, sponges, and algae. Pyramidellid snails are particularly invasive, exploiting the clams by inserting their proboscises (*i.e.,* feeding appendage) into the clam tissue and consuming the hemolymph within the siphonal mantle (Braley, 1992). On rare occasions, the snails may prove fatal to juvenile clams, but they are unlikely to cause mortality in adult clams (Mies, Scozzafave, *et al.,* 2017). Other external parasites (*i.e.,* sponges and algae) are typically more of a nuisance to giant clams rather than fatal infestations. For instance, boring sponges (*e.g., Cliona)* may drill holes into the clam's shells, and algae (*e.g., Gracilaria* sp.) may overcrowd the shell and prevent the mantle from extending, but neither of these parasites typically cause mortality (Mies, Scozzafave, *et al.,* 2017).

When disease is present, giant clams exhibit physical symptoms that are usually quite obvious, including a retracted mantle (typically the initial symptom), a gaping incurrent siphon (indicative of more advanced disease), and discarding of the byssal gland (Mies, Scozzafave, *et al.,* 2017). While some diseases may respond to antibiotics, concentrations and dosages for giant clams have not been well studied. Overall, the prevalence and

severity of disease likely vary across the extensive range of giant clams, but there is no information to indicate that disease is an operative threat to giant clams to the extent that it is significantly increasing the extinction risk of the species addressed here.

Much of what is known regarding predation of giant clams has been learned from the ocean nursery phase of mariculture activities, when juveniles are outplanted to their natural environment (Govan, 1992). Giant clams are widely exploited as a food source on coral reefs, with 75 known predators that employ a variety of attack methods (see table 3 in Neo, Eckman, *et al.* (2015) for a comprehensive list). These predators are largely benthic organisms, including balistid fishes, octopods, xanthid crabs, and muricid gastropods (Govan, 1992). The fishes (*e.g.,* wrasse, triggerfish, and pufferfish) prey on both juvenile and adult giant clams by biting the mantle edge, the exposed byssus, or extended foot. Other predators (*e.g.,* crabs, snails, and mantis shrimp) have been observed chipping, drilling holes into, and/or crushing the shells of smaller individuals (see review in Neo *et al.* 2015). Heslinga *et al.* (1984) observed several instances of predation firsthand in association with giant clam culturing operations in Palau. Large muricid snails (*Chicoreus ramosus*) were found to attack, kill, and eat *T. squamosa* specimens up to at least 300 mm shell length, and a single hermit crab was able to crush 26 *T. gigas* juveniles (20–30 mm) when inadvertently left in the culture tank. The authors also noted circumstantial evidence of predation by *Octopus* spp. in Palau based on the characteristically chipped shells of giant clams often observed outside of octopus dens.

Giant clams employ a suite of defense mechanisms, both morphological and behavioral, to resist predatory attacks (Soo & Todd, 2014). For example, their large body size, small byssal orifice, and strong shells create physical barriers to predation. In addition, *T. squamosa* is equipped with hard, scaly projections on its shell known as scutes that have been shown to provide protection from crushing predators (Han *et al.,* 2008). Giant clams also exhibit behavioral defense mechanisms, such as aggregation, camouflage, rapid mantle withdrawal (Todd *et al.,* 2009) and squirting water from siphons (Neo & Todd, 2010). While the ability of giant clams to endure intense predation pressure and acclimate to repeated disturbance can have implications on their survival, these attributes have not been studied extensively (Soo & Todd 2014). Similar to disease, we find no

evidence to indicate that predation presents a significant threat to the extinction risk of the giant clam species addressed here.

The Inadequacy of Existing Regulatory Mechanisms

Giant clams are protected from overutilization to varying degrees by a patchwork of regulatory mechanisms implemented by the many countries, territories, and Tribal entities within their range. These local-scale measures are also supplemented by CITES international trade regulation, and in some areas, by multi-national initiatives aimed at supporting sustainable regional giant clam fisheries. We address each of these regulatory mechanisms in the following section and also include a brief discussion of international climate change regulations in the context of their potential effects on the extinction risk of giant clams. More detailed information on these management measures can be found in the accompanying Status Review Report (Rippe *et al.,* 2023).

Local Regulations

There is national legislation in place in more than 30 countries and territories specifically related to the conservation of giant clams. Many also provide indirect protection via marine parks and preserves or ecosystem-level management plans. In general, management of giant clam populations has been most effective in Australia, where early harvest prohibitions and strict enforcement have been largely successful in stabilizing giant clam population declines and limiting illegal poaching (Wells *et al.,* 1983; Dawson, 1986; Lucas, 1994). Many Pacific island nations have also implemented strict measures to mitigate fishing pressure on giant clams. These include total bans on commercial harvest and export of giant clams (*e.g.,* Fiji, Papua New Guinea, Solomon Islands, Vanuatu, FSM, Guam, Republic of Kiribati and Palau), minimum size limits for harvest (*e.g.,* French Polynesia, Niue, Samoa, American Samoa, Guam, and Tonga), harvest quotas or bag limits (*e.g.,* New Caledonia, the Cook Islands, and Guam), and gear restrictions on the use of SCUBA or certain fishing equipment (Andre´foue¨t *et al.,* 2013; Kinch & Teitelbaum, 2010; Neo *et al.,* 2017). We are not aware of any local regulations in place restricting the harvest of giant clams in CNMI, although the harvest of all coral reef-associated organisms in Guam and CNMI is managed under the 2009 Fishery Ecosystem Management Plan for the Mariana Archipelago.

In many Pacific islands, national legislation is also supplemented or enforced by way of customary fishing rights and marine tenure systems. This is the case in parts of Fiji, Samoa, Solomon Islands, Cook Islands, Papua New Guinea, and Vanuatu, where indigenous village groups hold fishing rights and regulate access to adjacent reef and lagoon areas (Govan *et al.,* 1988; Fairbairn, 1992a, 1992b, 1992c; Wells, 1997; Foale & Manele, 2004; Chambers, 2007; UNEP–WCMC, 2012). The rights of each Tribal group over its recognized fishing area include the right to carry out and regulate subsistence fishing activities. In certain circumstances, a local village or villages may impose temporary area closures to reduce harvesting pressure and allow giant clam stocks to recover (Foale & Manele, 2004; Chambers, 2007).

The effectiveness of these measures to address overutilization, however, is variable, and with limited capacity for long-term monitoring programs in the region, it can be difficult to properly assess. In general, anecdotal reports indicate that giant clam populations throughout the Indo-Pacific region continue to face severe stress (Neo *et al.,* 2017).

In the Philippines, for example, numerous reports following the giant clam export ban in 1990 suggested problems with enforcement, particularly within Badjao communities. The Badjao people live a predominantly seaborne lifestyle and are spread across the coastal areas of the southern Philippines, Indonesia, and Malaysia, with a total population estimated to be around one million (Government of the Philippines National Statistics Office, 2013; Rincon, 2018). Many in these communities were encouraged by buyers to collect and stockpile giant clam shells in the hope that the ban on giant clam export would eventually be lifted (Salamanca & Pajaro, 1996; Wells, 1997). Middlemen would reportedly advance money and provisions to fishermen on the condition that the shells be sold to them exclusively. The Badjaos would then harvest clams, consume or discard the meat and stockpile the shells (Salamanca & Pajaro, 1996). The non-compliance was exacerbated by varying interpretations of the law by Philippine authorities, who issued numerous CITES export permits in 1991–1992 under the presumption that the law excluded 'preban stock' (Wells, 1997). The ban was ultimately never lifted, and CITES reports indicate that the legal export of giant clams has ended in the Philippines. However, a recent report by the Wildlife Justice Commission (2021)

found that authorities have continued to find stockpiles of giant clam shells throughout the country. Authorities have made 14 seizures from 2016 to 2021, including of a 132,000-ton stockpile in the southern Philippines in October 2019 and several stockpiles in the Palawan area, one of the centers of giant clam abundance in the region. It is unclear how many of the shells were collected prior to the ban in 1990 versus how many were collected illegally in the years since, but it suggests that the market for giant clam shells remains active more than 30 years after the ban was instituted. In an interview with ABS–CBN News (2021), Teodoro Jose Matta, executive director of Palawan Council for Sustainable Development, claimed that the clams are being smuggled to Southeast Asia and Europe and attributed the activities to a criminal syndicate operating across the Philippines, not just in Palawan. To our knowledge, these claims have not been corroborated by authorities.

Similar confusion over giant clam harvesting regulations has impeded the effectiveness of regulations to address overutilization in Papua New Guinea. An initial ban on the purchase and export of wild-caught giant clams was put in place in 1988 by the Department of Environment and Conservation (DEC) (Kinch, 2002; UNEP–WCMC, 2011). It was lifted in 1995 following the development of a management plan for sustainable harvest; however, Kinch (2002) noted that although the Milne Bay Province Giant Clam Fishery Management Plan had been drawn up by the National Fisheries Authority (NFA)—the CITES Scientific Authority for Papua New Guinea—it was never officially adopted ''owing to confusion between the NFA and the DEC over responsibility for the enforcement of the plan and because of opposition from commercial and political interests.'' The ban was reinstated in 2000 following reports that a local fishing company was exporting wild-caught specimens as captive-bred. Kinch (2002) suggested that further ''conflict and confusion between the fisheries and environmental legislation'' ensued and recommended that it be addressed to ensure success of the regulation. Unfortunately, the last known monitoring survey in Papua New Guinea was conducted in 1996 in the Engineer and Conflict Island Groups. Based on survey findings, it was estimated that the overall density of giant clams (all local species) had declined by over 82 percent since the early 1980s, while the density of *T. gigas* had declined by over 98 percent

(Ledua *et al.,* 1996). Without more recent data, we cannot determine whether the regulatory actions have had any effect on this trajectory.

Furthermore, despite various levels of harvest and export prohibitions among many of the Pacific island nations, Kinch and Teitelbaum (2010) highlight a number of common challenges to ensuring sustainable giant clam management in these communities. This includes a lack of capacity for conducting stock assessments, promoting giant clam mariculture, enforcing harvesting regulations, and monitoring and actively managing giant clam harvest. The list also includes a lack of education and awareness among community members about sustainable giant clam harvest, uncoordinated legislative structure, and a lack of international collaboration to promote a sustainable and scalable market for captive-bred giant clams. According to the assessment by Kinch and Teitelbaum (2010), each of the countries experiences these challenges to a different degree, but overall it highlights the difficulties in effectively managing giant clam populations for smaller island nations that may lack enforcement resources or expertise. This is compounded, in many cases, by the traditional importance of giant clams as a coastal resource, which may limit the willingness among indigenous communities to adopt the recommended practices (Neo *et al.,* 2017).

In addition to the two examples above, there are a number of other reports highlighting the inadequacy of local regulations to address the threat of overutilization throughout Indo-Pacific region. In Malaysia, and particularly in Borneo, illegal collection of giant clams was reported to occur despite a national prohibition on the collection of giant clams (Ibrahim & Ilias, 2006). In the Solomon Islands, commercial harvest and export was banned in 1998, but CITES records indicate that export of wild-sourced clams and shells from the Solomon Islands has continued to occur throughout the 2000s and as recently as 2015. Yusuf and Moore (2020) note that despite being fully protected under Indonesian law and widespread public awareness of associated harvest prohibitions, giant clams are still harvested regularly in the Sulawesi region of Indonesia, including mass collections for traditional festivals. When asked about enforcement of legal protections, locals explained that surveillance in certain areas was generally absent (or at best sporadic and ineffective), and throughout the region was ''minimal, often perceived as misdirected and/or unfair, and mostly

ineffective.'' Due in part to the ineffectiveness of the existing regulations, Yusuf and Moore (2020) have documented progressive declines in giant clam populations from 1999 to 2002, 2007, and 2015, with ''some larger species (*T. gigas, T. derasa, T. squamosa,* and *H. porcellanus*) no longer found at many sites.'' Low abundance of *T. squamosa, T. derasa, T. gigas,* and *H. hippopus* has also been observed in the Anambas Islands of Indonesia, where Harahap *et al.* (2018) report ongoing harvesting and habitat destruction. In Mauritius, giant clams are protected under the Fisheries and Marine Resources Act of 2007, but a recent study shows continued population declines even within marine protected areas (Ramah *et al.,* 2018). There are few studies highlighting success of local regulations, but Rossbach *et al.* (2021) report based on interviews with local fishermen that giant clams are no longer targeted in Saudi Arabia since a harvest prohibition was imposed in the early 2000s. Although we note that giant clams were listed as ''Taxa of High Conservation Priority'' in Saudi Arabia's First National Report to the Convention on Biological Diversity in 2004 (AbuZinada *et al.,* 2004), we could not find any national regulations associated with this designation.

The general lack of long-term monitoring data makes it difficult to evaluate the effectiveness of local regulatory mechanisms to address threats from overutilization for commercial purposes beyond relying on anecdotal reports. In many areas, for example, harvest prohibitions have been instituted within the last decade or two, but there have been few, if any, followup surveys conducted in the time since. However, using what survey data are available, we can infer that existing regulations have been inadequate to protect any of the seven giant clam species from overutilization. Despite widespread commercial export bans, the capacity for enforcing existing regulations is often limited, existing regulations do not restrict continued subsistence harvest in many locations, and illegal harvest and trade of giant clams (particularly for the shell trade) continues to occur (Kinch & Teitelbaum, 2010; Yusuf & Moore, 2020; Wildlife Justice Commission, 2021). For these reasons, we conclude that the inadequacy of local harvest regulations to address overutilization associated with subsistence fisheries and illegal harvest in all locations outside of Australia contributes significantly to the long-term extinction risk of *H.*

hippopus, T. derasa, T. gigas, and *T. squamosa.* Moreover, considering the exceptionally low abundance and restricted ranges of *H. porcellanus* and *T. mbalavuana,* we conclude that the inadequacy of local harvest regulations to address overutilization associated with subsistence fisheries likely also poses a short-term risk of extinction for these species in the near future.

With respect to *T. squamosina,* we also considered the likely effect of marine protected areas (MPAs), which are the principal regulatory mechanism relevant to the protection of giant clams from overutilization in the Red Sea. Based on the known distribution of *T. squamosina,* there are three MPAs that are most relevant to the species: Ras Mohammed National Park in South Sinai, Aqaba Marine Park in Jordan, and the Farasan Islands Protected Area in southern Saudi Arabia. These are three areas where *T. squamosina* has previously been observed, and remaining populations likely benefit from the prohibitions against hunting or collecting wildlife within the boundaries of the MPAs. According to Gladstone (2000), a prohibition on the collection of giant clams in the Farasan Islands appeared to be effective, with harvest-related mortality falling to 1.7 percent, compared to an estimated 11.1– 47.8 percent mortality rate prior to the regulation. Ras Mohammed National Park is also regarded as effective in the protection of 345 km² of marine area, which includes important fringing reef habitats in the southern portion of the Gulf of Aqaba.

Collectively, however, these three protected areas encompass only a small fraction $(5,756 \text{ km}^2)$ of the coastal marine area in the Red Sea. Throughout most of the region, harvest of giant clams remains largely unregulated. As is described above, historical harvest of giant clams has likely led to the exceptionally low abundance of *T. squamosina* in the Red Sea, and there are reports that harvest is ongoing in most locations. Thus, given the lack of national regulations pertaining to the harvest of giant clams in the Red Sea, we find that an inadequacy of existing regulatory mechanisms to address the threat of overutilization contributes significantly to the long-term extinction risk for *T. squamosina.* However, because several MPAs have been established in key areas where the species has been recently observed, we conclude that this factor does not in itself constitute a danger of extinction in the near future.

Regulations for International Trade

Giant clams are listed under appendix II of CITES, which consists of species that ''are not necessarily now threatened with extinction, but may become so unless trade is closely monitored.'' This designation does not necessarily limit trade of the species, but instead requires that any species in trade has been legally acquired and a finding that trade is not detrimental to the survival of the species by the exporting Party's Scientific Authority. CITES regulates all international trade in giant clams (including living, dead, and captivebred specimens) and requires the issuance of export permits and re-export certificates. For each listing, a Party may take a reservation to that listing, meaning the Party will not be bound by the provisions of the Convention relating to trade in that species. While the reservation is in effect, the Party is treated as a non-Party regarding trade in the particular species. Currently, Palau has reservations on all of the giant clam listings. Parties with reservations or other non-Parties that trade with a CITES Party are required to have documentation comparable to CITES permits. It is up to the Party State receiving the export whether to accept this documentation in lieu of CITES permits.

Effective enforcement of CITES is largely dependent on whether the countries involved are signatories to the Treaty, as well as the accuracy of trade data supplied by the Parties (Wells, 1997). Of the 60 countries and territories where the seven giant clam species considered here naturally occur, 52 are signatories to the Treaty. This includes the United States and all of its Pacific island territories. A number of countries that have historically played a significant role in the trade of giant clam products are not CITES contracting parties (*e.g.,* Cook Islands, Kiribati, Marshall Islands, FSM) or have only become so relatively recently (*e.g.,* Palau in 2004, Solomon Islands in 2007, Maldives in 2012, Tonga in 2016). However, all CITES Parties trading in CITES listed species with countries that are not members of CITES, or with CITES Parties that have taken a reservation on the species, must still seek comparable documentation from the competent authorities of the reserving Party or the non-member country, which substantially conforms with the usual requirements of CITES for trade in the species. Importantly, even in instances where exporting countries are Parties to CITES, the trade data must be interpreted cautiously for reasons that may include frequent

discrepancies in recorded import and export quantities, inconsistencies in the terms or units used to describe the trade, occasional omissions of seized or confiscated specimens, erroneous data entry, and delays or failure to submit trade statistics to the Secretariat (UNEP– WCMC, 2012; CITES, 2013; Neo *et al.,* 2017).

Overall, the threat of inadequate regulations related to the international trade of giant clam products is relevant only to the species that are traded in significant quantities. This does not include *T. mbalavuana* or *T. squamosina,* as we could not find any information to indicate that there has ever been an international commercial export market for these species. With respect to *H. hippopus, T. derasa,* and *T. squamosa,* CITES annual report data indicate that the large majority of recent international trade of these species is of culture-raised specimens and products. Since 2010, only 2,756 *H. hippopus* shells and 7,302 live *H. hippopus* specimens have been recorded in trade. Approximately 51.2 percent of traded shells during this period were of wildcaught origin, primarily from the Solomon Islands in 2014, while 34.1 percent were reportedly culture-raised. Of the live specimens, only 2.6 percent were wild-caught, while 96.2 percent were reportedly culture-raised.

Similarly, since 2010, 154,245 of the 158,319 live *T. derasa* specimens recorded in trade were culture-raised (97.4 percent), while only 3,514 were reportedly wild-caught (2.2 percent). A smaller proportion of shells and shell products recorded in trade since 2010 were of cultured *T. derasa,* but the total trade volume is significantly lower. In total, 3,775 of the 11,100 *T. derasa* shells and shell products were of culture-raised specimens (34 percent), while 7,312 were wild caught (65.9 percent).

The primary market for *T. squamosa* in international trade is of live clams for the ornamental aquarium industry, and it appears that most major exporters have transitioned their supply to cultured specimens. The major exceptions are Cambodia and Vietnam, which together have exported over 50,000 wild-caught *T. squamosa* since 2010. The government of Vietnam instituted a quota system to regulate the commercial harvest of wild giant clams after concerns were raised in the early 2010s about the level of exploitation. However, the subsequent rise in the export of live *T. squamosa* from Cambodia to Vietnam suggests that this regulation simply diverted the harvest to neighboring waters. While this harvest pressure likely threatens the

persistence of *T. squamosa* populations in Cambodia in the long term, available reports suggest that the species is still frequent in both countries.

Based on these data, we conclude CITES regulations have been effective at transitioning much of the international supply of *H. hippopus, T. derasa,* and *T. squamosa* products away from wild harvest and towards mariculture operations and therefore, minimizing the risks to these three species from overutilization associated with international trade. In other words, it is unlikely that this factor contributes significantly to the extinction risk for these species.

With respect to *H. porcellanus,* only five shells have been recorded in international trade since 2010—two exported from Malaysia to the Netherlands in 2013, and three exported from the Philippines and seized in the United States in 2011 and 2016. However, it is likely that the low trade levels are as much a reflection of the species' low abundance as they are of the effectiveness of international regulation. Regardless, although commercial trade of this species significantly reduced its abundance in the past, there is little evidence to suggest that international trade is a threat currently operating on this species, and given the available information to suggest otherwise, the regulations appear to be adequate to address that threat.

With respect to *T. gigas,* unlike *H. hippopus* and *T. derasa,* CITES records indicate that the majority of the reported trade since 2010 is of wild-caught specimens, suggesting that mariculture has not played a significant role in diverting harvest away from wild populations. As recently as 2018, Indonesia exported 59,000 wildharvested *T. gigas* shells to China despite the reportedly low abundance of *T. gigas* throughout the region and despite both nations being CITES contracting Parties. While most countries and territories within the range of *T. gigas* are regulated under the provisions of CITES, the associated protections were clearly not adequate to prevent widespread population loss and local extirpations of the species from many of the same locations (Neo *et al.,* 2017). Thus, we conclude that inadequate regulation of international trade to address the threat of overutilization contributes significantly to the long-term extinction risk of *T. gigas.*

Regulations on Climate Change

In the final rule to list 20 reef-building corals under the ESA (79 FR 53851), we

assessed the adequacy of existing regulatory mechanisms to reduce global greenhouse gas (GHG) emissions and thereby prevent widespread impacts to corals and coral reefs. We concluded that existing regulatory mechanisms were insufficient to effectively address this threat. Since the publication of that final rule in 2014, 197 countries and the European Union (EU) adopted the Paris Agreement on climate change, which set a goal of limiting the global temperature increase to below 2 °C and optimally keeping it to 1.5 °C. Since the Agreement was entered into force on November 4, 2016, 191 countries and the EU have ratified or acceded to its provisions, and each Party has made pledges to decrease GHG emissions to achieve its goals (UNFCC, 2018). The United States, which currently accounts for one-fifth of the world's emissions, pledged to cut its emissions by 26–28% percent. However, according to the 2023 Synthesis Report for the IPCC's Sixth Assessment Report, there remains a ''substantial emissions gap'' between the projected emissions trajectory associated with the climate actions currently proposed by the Parties to the Paris Agreement and the trajectories associated with mitigation pathways that limit warming to 1.5 C or 2 C by 2100 (IPCC 2023). The IPCC reported with high confidence that current limited progress towards GHG emissions reduction make it likely that warming exceeds 1.5 °C by 2100 and make it considerably harder to limit warming to less than 2 °C. In addition, the IPCC projected with medium confidence that the current emissions trajectory without strengthening of policies will lead to an estimated global temperature increase of 3.2 °C by 2100, with a range of 2.2 \degree C to 3.5 \degree C (IPCC, 2023).

At this rate, unless average emissions reduction goals are significantly strengthened, van Hooidonk *et al.* (2016) project that over 75 percent of reefs will experience annual recurrence of severe bleaching events before 2070. In a similar analysis, Hoegh-Guldberg *et al.* (2007) investigated four emissions reduction pathways that are used by the Intergovernmental Panel on Climate Change and found that only the most aggressive scenario would allow the current downward trend in coral reefs to stabilize. The study predicts that even moderate emission reductions will still lead to the loss of more than 50 percent of coral reefs by 2040–2050. Thus, regardless of whether the goals of the Paris Agreement are met, impacts to coral reefs are expected to be widespread and severe. However, as is

discussed above, while there is clear evidence that coral reefs will undergo substantial changes as a result of ocean warming and acidification, it is unclear whether and to what degree the changes in coral reef composition and ecological function will threaten the survival and productivity of giant clams. Furthermore, as is discussed below in *Other Natural or Man-Made Factors,* there is substantial evidence to suggest that giant clams may experience significant physiological changes under projected ocean warming scenarios. The precise magnitude of these impacts is unknown, but any significant changes in metabolic demand, reproductive success, and the possibility of bleaching due to warming summer temperatures, will likely increase the risk of extinction. For this reason, we find with respect to all seven species that the inadequacy of regulations to address climate change may, in combination with the aforementioned impacts, contribute significantly to the long-term or near future risk of extinction, but is unlikely a significant threat on its own.

Inadequacy of Regulations in the South China Sea

As is discussed above, *H. hippopus, H. porcellanus, T. gigas,* and *T. squamosa* also face the threat of habitat destruction in portions of the South China Sea where fishermen, primarily from the Hainan Province of China, have been razing shallow reef areas in a search for giant clam shells (see *Present or Threatened Destruction, Modification, or Curtailment of Its Habitat or Range*). In an effort to curtail this destructive activity, the Hainan Province People's Congress passed regulations in January 2017 to prohibit the commercial trade of all giant clam species in the province. However, a recent report from the Wildlife Justice Commission (2021) suggests that the illegal harvest and trade of giant clam shells continues to occur in the region, with new harvesting boats returning to the Hainan Province since 2018. For this reason, we conclude that the inadequacy of existing regulations to address the threat of habitat destruction in the South China Sea due to giant clam shell harvesting operations contributes significantly to the longterm extinction risk of *H. hippopus, T. gigas,* and *T. squamosa.* In addition, due to the exceptionally low abundance and highly restricted range of *H. porcellanus,* which includes the southern portion of the South China Sea, the combination of these threats likely also contributes to the near future extinction risk for *H. porcellanus.*

Other Natural or Man-Made Factors

There are several other natural or manmade factors that impact giant clams, such as ocean warming and acidification, coastal pollution and sedimentation, and stochastic mortality events. Below, we summarize each of these factors, and where sufficient information is available, evaluate the severity of the associated threat to each of the seven giant clam species.

Ocean Warming

As is mentioned above, giant clams associate symbiotically with a diverse group of dinoflagellates of the family Symbiodiniaceae which reside within a network of narrow tubules that branch off the primary digestive tract and spread throughout the upper layers of the mantle (Norton *et al.,* 1992). Giant clams provide dissolved inorganic nutrients to the zooxanthellae via direct absorption from the seawater or as an excretory byproduct of respiration, and in return, receive photosynthetic carbon in the form of glucose, glycerol, oligosaccharides and amino acids, comprising the majority of their metabolic carbon requirements (Klumpp *et al.,* 1992; Hawkins & Klumpp, 1995). Exposure to stressful environmental conditions, however, can cause dysfunction in the symbiosis and, in extreme cases, can lead to a bleaching response wherein the zooxanthellae is expelled from the mantle tissue. When they bleach, giant clams lose a critical source of nutrition and experience drastic changes to their physiology, including decreased glucose and pH in the hemolymph, an increased concentration of inorganic carbon (*e.g.,* $CO₂$ and HCO₃-), and a reduced capacity for ammonium assimilation (Leggat *et al.,* 2003).

Elevated temperatures, in particular, are known to induce bleaching in giant clams. Widespread bleaching of giant clams was observed in the central Great Barrier Reef, Australia in 1997–1998, when elevated water temperatures in conjunction with low salinity caused 8,000 of 9,000 surveyed *T. gigas* to experience varying levels of bleaching (Leggat, pers. comm., cited in Buck *et al.,* 2002; Leggat *et al.,* 2003). Some individuals suffered a complete loss of symbionts, while others were only affected in the central part or at the margins of the mantle tissue (Grice, 1999). A follow-up experiment designed to replicate the environmental conditions during this event demonstrated that elevated temperatures combined with high solar irradiance induced a consistent bleaching response in *T. gigas* (Buck *et*

al., 2002). Populations of *T. squamosa* around Mannai Island, Thailand also suffered extensive bleaching in mid-2010 due to prolonged exposure to temperatures averaging 32.6 °C (Junchompoo *et al.,* 2013). Bleaching was recorded in every *T. squamosa* specimen observed $(n = 12)$, of which only four individuals recovered while the remaining two-thirds died (Junchompoo *et al.,* 2013).

While the appearance is similar to the bleaching response observed in corals, bleaching of giant clams is unique in two important ways. First, the mechanics differ on account of the zooxanthellae residing extracellularly in giant clams. Rather than being expelled from host cells, as is the case with corals, zooxanthellae are thought to be driven out of the giant clam tubular system via long cilia and expelled through the digestive tract (Norton & Jones, 1992; Norton *et al.,* 1995). The expulsion of algal cells is associated with atrophy of the tertiary zooxanthellae tubes, which is thought to inhibit the return of the zooxanthellae to the host clam (Norton *et al.,* 1995). According to one account, some adult *T. gigas* have remained partially bleached for more than a year (R. Braley, pers. comm., cited in Norton *et al.,* 1995). Second, there is evidence that giant clams are more resilient to bleaching than corals and can tolerate temperature stress for longer (Grice, 1999; Buck *et al.,* 2002; Leggat *et al.,* 2003). According to Leggat *et al.* (2003), of 6,300 *T. gigas* that bleached at Orpheus Island, Australia in 1998, over 95 percent completely recovered after 8 months. Moreover, during the three global-scale coral bleaching events when anomalous warming caused widespread mortality of stony corals (1998, 2010, and 2014– 2017), reports of giant clam bleaching have been sparse and variable across species and geography. Neo *et al.* (2017) reported that in 2016, ''*Tridacna maxima* [which is not subject to this rulemaking] did not bleach in Mauritius (R. Bhagooli, pers. comm., cited in Neo *et al.,* 2017), but those in Singapore (M. L. Neo, pers. obs.), Guam (A. Miller, pers. comm., cited in Neo *et al.,* 2017), and East Tuamoto (S. Andréfouët, pers. comm., cited in Neo *et al.,* 2017) were bleached severely.'' At Lizard Island, Australia, *T. gigas* reportedly suffered ''much lower'' mortality than *T. derasa* and *T. squamosa* during the 2016 event (A.D. Lewis, pers. comm., cited in Neo *et al.,* 2017). Actual mortality rates were not provided.

Even in the absence of bleaching, warming-related stress can profoundly impact the growth and reproduction of giant clams. Growth rates in giant clams tend to follow a standard thermal performance curve whereby growth is positively correlated with temperature up to a thermal optimum (Pearson & Munro, 1991; Hart *et al.,* 1998; Schwartzmann *et al.,* 2011; Van Wynsberge *et al.,* 2017). Beyond this point, further warming can cause shell growth to become erratic and slow down significantly (Schwartzmann *et al.,* 2011; Syazili *et al.,* 2020). Excessive warming has also been shown to lower fitness by reducing photosynthetic yield (Brahmi *et al.,* 2021), altering the photosynthesis-respiration ratio (Braley *et al.,* 1992; Blidberg *et al.,* 2000; Elfwing *et al.,* 2001), reducing the strength and carbonate content of the shells (Syazili *et al.,* 2020), and reducing fertilization success (Armstrong *et al.,* 2020). Early life stages are thought to be particularly sensitive to these impacts, as warming has been shown to speed up the progression through early development, leading to abnormal development, reduced settlement, and lower overall juvenile survival (Watson *et al.,* 2012; Neo *et al.,* 2013; Enricuso *et al.,* 2019).

In assessing the contribution of ocean warming to the extinction risk of the seven species considered in this rulemaking, we relied on the best available scientific and commercial data relating to each species specifically. With respect to *H. hippopus,* results from a laboratory experiment in the Philippines showed that *H. hippopus* experienced a significant increase in respiration under elevated temperatures and was more sensitive to warming than the two other species tested (*T. gigas* and *T. derasa*). After 24 hours of exposure to elevated temperatures (3 °C above ambient), no bleaching was observed (Blidberg *et al.,* 2000). Additionally, Schwartzmann *et al.* (2011) documented the in situ response of *H. hippopus* to elevated temperatures in New Caledonia. At the end of the summer, the combination of high temperatures and high irradiance altered the growth and gaping behavior of *H. hippopus.* At the solar maximum, daily growth increments and gaping behavior became erratic, indicating some degree of physiological distress. The effect was pronounced when temperatures stayed above 27 °C, which is near the current summer maximum in this region.

The few studies available with respect to *T. derasa* found that juveniles suffered reduced photosynthetic production and respiration when exposed to warming of 3 °C, but neither bleaching nor mortality were reported (Blidberg *et al.,* 2000). Neo *et al.* (2017) also noted significant mortality of *T.*

derasa at Lizard Island, Australia following anomalous warming in 2016 that led to widespread coral bleaching and following three successive years of cyclones, but did not provide evidence directly tying the mortality to one cause or the other.

The best available scientific and commercial data suggest that *T. gigas* is sensitive to ocean warming at multiple life stages. For example, Enricuso *et al.* (2019) found that higher water temperatures (33 °C, compared to 28 °C and 30 °C) promote rapid progression through early development, but result in lower overall survival as a consequence of abnormal development and reduced post-settlement survival. Lucas *et al.* (1989) found that juvenile growth rate increased during summer months as temperatures rose to 30 °C, but noted that higher temperatures (33–35 °C) can lead to bleaching (Estacion & Braley, 1988). As is discussed above, widespread bleaching of *T. gigas* was observed in the central Great Barrier Reef, Australia in 1997–1998 (Leggat, pers. comm., cited in Buck *et al.,* 2002; Leggat *et al.,* 2003), later attributed to the combination of elevated temperatures with high solar irradiance (Buck *et al.,* 2002). Notably, according to Leggat *et al.* (2003), over 95 percent of the *T. gigas* that were observed to have bleached in 1998 completely recovered after 8 months, indicating that *T. gigas* can withstand the acute stress of bleaching if anomalous conditions are not prolonged.

With respect to *T. squamosa,* two similar studies used a cross-factorial experimental design to examine the synergistic effects of elevated temperature and $pCO₂$ on the survival and growth rate of juveniles. Watson *et al.* (2012) found that juvenile survival decreased with increasing temperature, with the lowest survival occurring at the moderate and highest seawater temperatures (30.0° and 31.5 °C, versus 28.5 \degree C) combined with the highest acidification treatment (1019 ppm $pCO₂$) versus 416 and 622 ppm). Likewise, Syazili *et al.* (2020) found that elevated warming significantly reduced juvenile growth rate, as well as the strength and carbonate content of the shell, based on temperature treatments of 30, 32, and 34 °C. However, a separate study by Armstrong *et al.* (2022) yielded conflicting results indicating that the growth rate of juvenile *T. squamosa* was unaffected by an increase in temperature. These findings were based on temperature treatments of 28.5 ° and 30.5 °C, meant to simulate present-day and end-of-century conditions. Elfwing *et al.* (2001) found that experimental warming enhanced respiration rate in *T.*

squamosa juveniles and, in effect, reduced the photosynthesis-respiration ratio. Elevated temperatures have also been shown to enhance fertilization success in *T. squamosa* but significantly reduce trochophore survival (Neo *et al.,* 2013). Only 3.6–13.9% of trochophores survived 24 hours of exposure to 29.5 °C compared to 32.5–46.8% survival at 22.5 °C.

Based on this information, we find it likely that ocean warming will negatively impact the fitness of *H. hippopus, T. derasa, T. gigas,* and *T. squamosa* in various ways and that it may, in combination with other threats and demographic risk factors, contribute to the long-term extinction risk for these species. However, given the limited information available and the variability in the reported impacts of ocean warming among studies and species, we cannot conclude with confidence that ocean warming on its own constitutes a significant long-term or near future extinction risk to *H. hippopus, T. derasa, T. gigas,* and *T. squamosa.*

With respect to *H. porcellanus, T. mbalavuana,* and *T. squamosina,* we could not find any specific information addressing the potential impacts of ocean warming beyond what is discussed above in regard to other giant clam species. Based on the information that is available for other species, we find that ocean warming may, in combination with other threats and demographic risk factors, contribute to the long-term extinction risk for *H. porcellanus, T. mbalavuana,* and *T. squamosina.* However, while we can broadly infer that ocean warming may negatively impact the fitness of these species in some respect, we are reluctant to make extrapolations from these studies about the specific nature or magnitude of the impact, as it is possible that susceptibility may vary significantly among species. For example, species like *H. porcellanus* or *T. squamosina,* which reside preferentially in shallow habitats where temperature fluctuations can be quite extreme, may have adapted a higher tolerance to such conditions. Given this uncertainty, we do not have sufficient information to conclude that ocean warming is a significant threat to *H. porcellanus, T. mbalavuana,* and *T. squamosina* on its own.

Ocean Acidification

There is concern that ocean acidification may also pose a significant risk to giant clams, based primarily on experimental evidence from other shelled mollusks. In two comprehensive literature reviews, both Parker *et al.* (2013) and Gazeau *et al.* (2013)

concluded that the consequences of ocean acidification for calcifying marine organisms (and mollusks in particular) are likely to be severe, as they rely on the uptake of calcium and carbonate ions for shell growth and calcification. Yet, while many studies have demonstrated a negative effect on the growth of marine mollusks, some species have shown no response or even a positive growth response to ocean acidification (Ries *et al.,* 2009; Gazeau *et al.,* 2013; Parker *et al.,* 2013).

With respect to giant clams specifically, experimental data on the effects of ocean acidification are limited and similarly inconclusive. Syazili *et al.* (2020) found that juvenile *T. squamosa* exhibited decreased growth and weaker shell structure under elevated $pCO₂$; however, Armstrong *et al.* (2022) found the opposite, that growth rates of juvenile *T. squamosa* were enhanced under acidification treatments. Watson *et al.* (2012) found that juvenile *T. squamosa* suffered greater mortality when exposed to elevated $pCO₂$ (see also Syazili *et al.,* 2020), and fertilization success of *T. maxima* was found to be unaffected (Armstrong *et al.,* 2020). Lastly, in comparing the growth and survival of four giant clam species in conditions approximating future ocean acidification scenarios, Toonen *et al.* (2011) found the responses to vary among species. *T. maxima* and *T. squamosa* had significantly lower growth rates in low pH, *T. derasa* had a significantly higher growth rate, and *T. crocea* was not significantly different between low pH and ambient seawater. The authors concluded that ''such strong species-specific differences and interactions among treatment variables [. . .] caution against broad generalizations being made on community effects of ocean acidification from single-species laboratory studies'' (Toonen *et al.,* 2011).

Furthermore, as is mentioned above, ocean acidification will likely not affect all regions uniformly, as seawater carbonate dynamics are highly dependent on many local-scale factors, such as temperature, proximity to landbased runoff, proximity to sources of oceanic $CO₂$, salinity, nutrients, as well as ecosystem-level photosynthesis and respiration rates. This makes it difficult to assess how ocean acidification is impacting giant clams currently or may impact them in the future. For this reason, and given the existing uncertainty regarding the effects of ocean acidification on giant clams, there is not sufficient information to further consider this potential threat in the extinction risk assessments for each species.

Land-Based Sources of Pollution

Giant clams are also susceptible to land-based sources of pollution, including sedimentation, elevated nutrients, salinity changes, and exposure to heavy metals. Together, these factors represent environmental conditions that giant clams may experience following heavy rains, particularly near coastlines that have been altered by human development. In its Sixth Assessment Report, the IPCC found that the frequency and intensity of heavy rainfall events has likely increased globally since the preindustrial era and projected that this trend is ''virtually certain'' to continue with additional global warming (Seneviratne *et al.,* 2021). The IPCC also found it ''likely'' that annual precipitation will increase over the equatorial Pacific and monsoon regions under a business-as-usual scenario, and projected with ''medium confidence'' that flooding and associated runoff will increase over parts of South and Southeast Asia by 2100 (Douville *et al.,* 2021). Thus, it is likely that giant clams will face an increasing occurrence of heavy rain events, runoff, and associated changes to water quality throughout much of their range.

Available evidence suggests that the impacts of sedimentation may vary between species. Reduced light levels associated with sedimentation have been shown to significantly decrease the growth rate of *T. squamosa* (Beckvar, 1981; Foyle *et al.,* 1997; Guest *et al.,* 2008), likely by limiting the photosynthetic potential of the symbiotic algae (Jantzen *et al.,* 2008; Przeslawski *et al.,* 2008). However, in situ observations from Pioneer Bay, Australia revealed that *T. gigas* actually grows faster in more turbid conditions compared to two offshore sites (Lucas *et al.,* 1989). These contrasting results may be indicative of differences in nutritional strategy between species (Klumpp *et al.,* 1992), suggesting that certain species are able to compensate for the reduction in photosynthetic yield by increasing the relative contribution of heterotrophy.

Giant clams are also sensitive to variations in salinity, nutrients, and heavy metal concentrations. Blidberg (2004) showed that a reduction in salinity significantly decreased the survival rates of *T. gigas* larvae. Only 1.1 percent and 2.2 percent of larvae survived when exposed to salinities of 20 parts per thousand (ppt) and 25 ppt, respectively, compared to a survival rate of 4.2 percent in the 32 ppt control. Maboloc *et al.* (2014) also found that lower salinity (18 ppt and 25 ppt vs. 35

ppt) reduced the feeding capacity of juvenile *T. gigas* due to alteration of the digestive membrane. The same effects, however, were not observed for *T. squamosa,* as a milder salinity reduction (27 ppt vs. 30 ppt) led to an increase in survival of *T. squamosa* trochophores and no significant effect on the survival *T. squamosa* embryos (Neo *et al.,* 2013).

Extreme reductions in salinity have been shown to alter the behavior of early life stages. *T. squamosa* trochophores and veligers stopped swimming and sank to the bottom of an experimental tank when exposed to salinities of 9 ppt and 12 ppt; although, once conditions returned to normal, the larvae resumed normal swimming functions within an hour (Eckman *et al.,* 2014). These results provide some evidence that giant clams may be able to withstand temporary salinity fluctuations. However, it is unlikely that they would experience such extreme conditions in situ. For example, in October 2010, immediately after a weeklong heavy rainfall in the Bolinao region of the Philippines brought by Typhoon Megi, salinity at a coastal giant clam nursery was measured to be 25 ppt (Maboloc *et al.,* 2014).

With respect to dissolved nutrients, there is consistent evidence that nitrogen enrichment increases the density of zooxanthellae in the clam tissue (Braley *et al.,* 1992; Belda, Lucas, *et al.,* 1993; Belda-Baillie *et al.,* 1999) and, in most cases, enhances the growth rate of giant clams. The addition of inorganic nitrogen led to a near doubling of the growth rate of young juvenile *T. derasa* (<1 cm) and a 20 percent increase in shell length in older juveniles over controls (Heslinga *et al.,* 1990). Similarly, *H. hippopus* juveniles exhibited a 110 percent increase in growth per month when exposed to elevated nitrogen (Solis *et al.,* 1988). Nitrogen enrichment has also been shown to enhance the shell and tissue growth of *T. gigas* (Belda, Cuff, *et al.,* 1993; Belda, Lucas, *et al.,* 1993).

Elevated heavy metals contribute to the environmental stress factors in contaminated waters near human development. For instance, in the Cook Islands, giant clams collected from the populated Pukapuka Atoll had significantly higher concentrations of iron, manganese, zinc, and lead than clams from the unpopulated Suvorov Atoll (Khristoforova & Bogdanova, 1981). Three related studies demonstrated that exposing *T. gigas, H. hippopus,* and *T. squamosa* to sublethal levels of copper (*T. gigas* and *H. hippopus:* 5 μg l⁻¹; *T. squamosa:* 50 μg l–1) reduces photosynthetic activity and, in effect, significantly lowers the

production-respiration ratio (Elfwing *et al.,* 2001; Elfwing *et al.,* 2002; Elfwing *et al.,* 2003). This aligns with previous work showing that copper acts as an inhibitor in photosynthesis (Cid *et al.,* 1995 cited in Elfwing *et al.,* 2001).

In most circumstances, however, it is unlikely that giant clams would experience only one of the aforementioned issues associated with land-based sources of pollution independent of the others. River outflows and runoff from heavy rain events will necessarily alter the salinity, and in most cases will also carry suspended sediments, dissolved nutrients, heavy metals, or a combination of the three to the nearshore environment. Blidberg (2004) suggests that synergistic effects of elevated heavy metal concentrations in combination with low salinity may be more detrimental to giant clams than either factor alone. At a relatively low dose of copper (2.5 mg l–1), *T. gigas* larvae survival was not significantly altered, but combined with a moderate reduction in salinity (25 ppt vs. 32 ppt), larval survival rate was decreased by nearly 75 percent. From these results, Blidberg (2004) hypothesized that chronically high copper concentrations and low salinity may explain the absence of giant clams near human settlements and river mouths.

Overall, the best available scientific and commercial data provide some indication that sedimentation, salinity changes, nutrient enrichment, and elevated heavy metal concentrations may impact the physiology and fitness of giant clams in certain respects. However, the effects are often not consistent between species and, in some cases, the experimental treatments do not reflect conditions that giant clams may realistically experience in the natural environment. Given this uncertainty and the likely localized nature of these impacts near areas of high runoff, we conclude that the threat of land-based sources of pollution is unlikely to contribute significantly to the extinction risk of any of the seven giant clam species considered here, either itself or in combination with other threats and demographic risks.

Stochastic Mortality Events

There have been several reports of mass mortalities of giant clams without a definitive cause. For example, reports from Lizard Island, Great Barrier Reef indicated that 25 percent of *T. gigas* and *T. derasa* died in a 6-week period in mid-1985, and over the following 18 months, total mortality rates were 55–58 percent (Alder & Braley, 1988). The authors ruled out toxins, predators,

environmental conditions, and old age as possible causes, and hypothesized that two pathogens that were observed (*Perkinsus* and an unknown protozoan) may be to blame. However, the findings were inconclusive, and the hypothesis was never confirmed. Extensive mortality was also reported in the early 1990s in the Solomon Islands, where *T. gigas* and *H. hippopus* were the main species affected (Gervis, 1992).

Mass mortality events represent a complex, unpredictable issue that can cause acute damage to giant clam populations with little forewarning. In each case, only certain giant clam species and certain areas were impacted by the mortality events, while other species, other bivalve mollusks, and other regions remained apparently unaffected (Lucas, 1994). For this reason, the extinction risk associated with these stochastic events is likely most significant for species with a restricted range or with few remaining populations, such as *H. porcellanus, T. mbalavuana,* and *T. squamosina.* However, the inherent unpredictability of these events affords little confidence in any assessment regarding the time scale of this threat. Overall, we conclude that the threat of stochastic mortality events may, in combination with low abundance, contribute significantly to the long-term extinction risk of *H. hippopus, H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina.* Considering the expansive range of *T. squamosa,* including several regions of relatively high abundance, we find it unlikely that this threat contributes significantly to the longterm or near future extinction risk of *T. squamosa* by itself or in combination with other threats or demographic risks.

Demographic Risk Analysis

Abundance

Because there are no global abundance estimates for the seven species considered here, we rely on the qualitative estimates of population status summarized in table 1, which are based on the best available survey data from all countries or territories where each species has been recorded.

H. hippopus

Available data indicate that *H. hippopus* has suffered significant population declines to the extent that the species is rare, extirpated, has been reintroduced after extirpation, or is data deficient (likely exceptionally rare or extinct) in 21 of 26 locations throughout its range. For broadcast spawning organisms like *H. hippopus,* which rely on the external fertilization of gametes,

the implications of such sparse distribution on reproduction can be significant. As is discussed above, Braley (1984) observed that 70 percent of nearest spawning giant clams (*T. gigas*) were found within 9 m of one another, while only 13 percent were between 20–30 m of one another. These findings suggest that individuals in rare populations are less likely to spawn in synchrony and as a result are likely to experience infrequent, sporadic reproductive success. This negative relationship between population density and productivity, known as the Allee effect, can cause further reductions in population abundance and put rare populations of *H. hippopus* at greater risk of extinction.

In 5 of the 26 locations where *H. hippopus* has been recorded, the species is considered frequent, indicating population density estimates that are between 10 and 100 ind ha–1. This includes the Great Barrier Reef, outlying islands of NW Australia, the Marshall Islands, Vanuatu, and Palau. Of these locations, only Australia has in place a total ban on the harvest of *H. hippopus.* The other countries have instituted a ban on the commercial export of giant clams, but subsistence harvest is still ongoing. In Vanuatu, *H. hippopus* is considered a prized subsistence food and is harvested regularly for household consumption and special occasions. Zann and Ayling (1988) reported that *H. hippopus* was overharvested on inhabited islands in Vanuatu and secure on only two reefs; it is unknown if these remote populations have been subjected to harvest in the three decades since the observations were published. Similarly, in the Marshall Islands, available reports suggest that giant clams are heavily exploited near population centers, and *H. hippopus* was reported to be abundant only on three remote atolls. Thus, in Vanuatu and Marshall Islands, overutilization remains a significant threat to *H. hippopus* populations. In Palau, the most recent survey from Helen Reef, a remote uninhabited atoll in the Western Caroline Islands was conducted in 1976, when the standing stock of *H. hippopus* was estimated to be over 70,500 (or 40.1 ind ha–1) (Hirschberger, 1980). However, due to its remoteness from the inhabited islands of Palau and the difficulty of surveilling the area, Helen Reef was historically targeted by giant clam poachers in the 1970s. While we are not aware of any more recent poaching in the area, it is possible that such activities have gone undetected. Thus, the current status of *H. hippopus* at Helen Reef is unknown. A recent survey

from the main island group in Palau (Rehm *et al.,* 2022) recorded an average population density of 51.5 ind ha–1, but the authors note that harvest of *H. hippopus* in this area is still ''very common.'' In Australia, there are very limited survey data on the abundance of *H. hippopus* on the Great Barrier Reef; however, anecdotal reports commonly suggest that populations of giant clams in general are healthy relative to other areas of the Indo-Pacific. Additionally, there is evidence that existing regulations have been effective at preventing illegal harvest and minimizing the risk of overutilization of giant clams in Australian waters. Several reports have suggested significant population declines from 1999 to 2009 at Ashmore and Cartier Reefs, two islands in NW Australia that have historically had abundant *H. hippopus* populations. The cause of the decline and current status of these populations is unknown.

Thus, while we consider *H. hippopus* to be frequent in 5 of the 26 locations where it occurs naturally (*i.e.,* where it has not been artificially introduced), in 2 of these locations (Vanuatu and the Marshall Islands), available reports indicate only a few remote sites have relatively abundant populations. The abundance of *H. hippopus* outside of these remote sites, particularly near human population centers, is considerably lower and is subject to the ongoing threat of unregulated domestic harvest. Populations of *H. hippopus* in Palau, NW Australia, and on the Great Barrier Reef appear to be healthy, despite ongoing harvest in Palau. Considering these locations alongside the 21 other locations in the species' range where overutilization has driven *H. hippopus* to low abundance, we find that this factor likely contributes significantly to the species' long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future.

H. porcellanus

Although quantitative abundance estimates are limited, the best available scientific and commercial data suggest that *H. porcellanus* has suffered significant population declines since the 1970s, leading to low abundance and very few remaining populations throughout its historical range. Only 55 individuals have been observed and recorded in published surveys since 1989, and recent reports suggest that the species has disappeared from most areas of the Philippines and Indonesia, which were once the core of this species' distribution. Only two sites, Tubbataha Reefs Natural Park in the Philippines

and Raja Ampat in Indonesia, are thought to have substantial populations of *H. porcellanus.* However, while there is some evidence that *H. porcellanus* may have recovered to an extent in Tubbataha Reefs after two decades of protection from harvest (Dolorosa & Jontila, 2012), the most recent survey data available are from 2008 and cover only 0.42 ha of the 96,828 ha in the park. Given the history of intense exploitation of this species in the Philippines and recent evidence of ongoing giant clam poaching in the region, we cannot conclude that this population has recovered to a sustainable level.

With so few remaining populations reduced to such a small fraction of the species' historical range, *H. porcellanus* is highly susceptible to the ongoing and future threats described above, including coastal development, ongoing harvest, the inadequacy of existing regulations, potential physiological impacts of ocean warming, and stochastic mortality events. Continued population reductions due to these factors threatens the persistence of remaining populations, and in effect, significantly elevates the extinction risk of *H. porcellanus.* For this reason, we find that the species' low abundance puts it in danger of extinction in the near future.

T. derasa

The best available scientific and commercial data indicate that *T. derasa* has suffered significant population declines to the extent that the species is considered rare, extirpated, or has been reintroduced after extirpation in 15 of the 18 locations throughout its range. As is discussed with respect to *H. hippopus,* such sparse distribution can significantly reduce reproductive success by disrupting spawning synchrony and minimizing fertilization rates. In every location where *T. derasa* is considered rare, subsistence harvest is still permitted or existing harvest bans, such as in Indonesia and the Philippines, have largely been ineffective at eliminating illegal harvest. In these locations, the low abundance of *T. derasa* exacerbates the extinction risk associated with continued harvest pressure.

Of the 18 locations where *T. derasa* occurs naturally (*i.e.,* where it has not been artificially introduced), there are only 3 locations where reports indicate that the species is likely frequent—these are the Great Barrier Reef, outlying islands of NW Australia, and Palau. Both locations in Australia are subject to a total ban on the harvest of *T. derasa.* As is discussed with respect to *H.*

hippopus, while there are very limited recent survey data on the abundance of *T. derasa* on the Great Barrier Reef, anecdotal reports consistently suggest that populations of giant clams (including *T. derasa*) in Australia are healthy relative to other areas of the Indo-Pacific.

In NW Australia, population estimates of *T. derasa* are variable, ranging from 1.3 ind ha–1 at Ashmore Reef to 77.7 ind ha–1 at N Scott Reef (Skewes *et al.,* 1999). In Palau, there is a ban on the commercial export of giant clams, but harvesting for subsistence and domestic sale is still reportedly very common, and *T. derasa* remains a highly desired food item, leaving these populations at risk of overutilization.

Overall, the abundance of *T. derasa* is greatly reduced from historical levels throughout its range, leaving only three locations where the species is not considered rare or extirpated. The species is at continued risk of overutilization in all locations where it is found, except for Australia, due to ongoing subsistence harvest and inadequate regulation. Based on this information, we find that the abundance of remaining populations contributes significantly to the species' long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future.

T. gigas

The best available scientific and commercial data indicate that *T. gigas* has suffered significant population declines to the extent that the species is considered rare, extirpated, has been reintroduced after extirpation, or is data deficient (likely exceptionally rare or extinct) in 32 of the 33 locations where it occurs naturally (*i.e.,* where it has not been artificially introduced). As is discussed above, such sparse distribution can significantly reduce reproductive success by disrupting spawning synchrony and minimizing fertilization rates. In every location where *T. gigas* is considered rare, except for NW Australia, subsistence harvest is still permitted or existing harvest bans, such as in Indonesia and the Philippines, have largely been ineffective at eliminating illegal harvest. In these locations, the low abundance of *T. gigas* exacerbates the extinction risk associated with continued harvest pressure.

Of the 33 locations where *T. gigas* occurs naturally, the only location where the species is considered ''frequent'' is the Great Barrier Reef in Australia. Populations on the Great Barrier Reef are protected by a total ban on the harvest of giant clams. As is

mentioned above, while there are very limited recent survey data on the abundance of *T. gigas* on the Great Barrier Reef, the data that are available, as well as anecdotal reports, consistently suggest that populations of giant clams (including *T. gigas*) in Australia are healthy relative to other areas of the Indo-Pacific.

Overall, the abundance of *T. gigas* is greatly reduced from historical levels throughout its range, leaving only one location where the species is not considered rare or locally extinct. Importantly, however, while we refer to the Great Barrier Reef as only one location, it covers an expansive geographic area that comprises a significant proportion of the suitable habitat within the species' range. Nonetheless, in all locations of its range outside of the Great Barrier Reef, *T. gigas* is at continued risk of overutilization due to ongoing subsistence harvest and inadequate regulation. Based on this information, we find that the abundance of remaining populations contributes significantly to the species' long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future.

T. mbalavuana

Although quantitative abundance estimates are lacking, the best available scientific and commercial data suggest that *T. mbalavuana* occurs at exceptionally low abundance and is sparsely distributed ''with single individuals being found at most locations'' (Ledua *et al.,* 1993). As part of a concentrated effort to collect broodstock specimens of *T. mbalavuana* for attempted spawning and larval culture, Ledua *et al.* (1993) estimated the number of clams found per manhour of search on SCUBA. The data showed that an average of about one clam per man-hour was collected in Tonga, while about 0.26 clams per manhour were collected in Fiji. There were only three sites where more than six clams were found, and all were around Ha'apai, Tonga, which the authors suggested may be the center of distribution for *T. mbalavuana* with the ''largest repository of the species.'' In total, 76 *T. mbalavuana* were observed and collected in Fiji and Tonga between 1986 and 1992 in more than 277 hours of searching.

Given its exceptionally low abundance, sparse distribution, and highly restricted range, *T. mbalavuana* is highly susceptible to the ongoing and future threats described previously, including continued domestic harvest, the inadequacy of existing regulations, and the possibility of future climate

change-related impacts to coral reef habitats. Potential population reductions due to these factors threatens the persistence of remaining populations, and in effect, significantly elevates the extinction risk of *T. mbalavuana.* For this reason, we find that the species' low abundance puts it in danger of extinction in the near future.

T. squamosa

Based on the best available scientific and commercial data, historical demand for *T. squamosa* meat and shells, ongoing demand for live specimens for the ornamental aquarium industry, and longstanding subsistence harvest has depleted *T. squamosa* populations in many areas of its range. Yet, despite the widespread exploitation, the global abundance of *T. squamosa* is relatively high compared to other giant clam species, with several locations where populations are likely frequent or abundant. This includes Australia (Great Barrier Reef), Indonesia, and the Philippines, which are the three locations with the most estimated coral reef area (and likely suitable habitat for *T. squamosa*) of all locations within the species' range. Of the 63 locations where *T. squamosa* occurs naturally, it is likely abundant in 5 locations, frequent in 14, rare in 32, and extirpated in 2 locations, with the other locations characterized as data deficient. Available reports suggest that abundance is particularly high in the Red Sea and in the South Asia regions, despite these areas being subject to widespread subsistence harvest and, in the case of South Asia, being at the center of the commercial shell and shell craft industry of the 1980s. Given the significant harvest pressure, this pattern suggests that *T. squamosa* populations in these regions are somewhat resilient to population declines, perhaps due to a large historical population size or due to high demographic connectivity facilitating larval exchange among connected populations within each region. Such a scenario would align with the genetic connectivity observed throughout the Indo-Malay Archipelago, discussed further in regard to the *Spatial Structure/Connectivity* risk below.

Overall, because the species occurs at relatively high abundance in a number of locations throughout its range, and especially in locations where the total area of coral reefs (and likely *T. squamosa* habitat) is relatively high, we find it unlikely that its abundance contributes significantly to the longterm or near-future risk of extinction by itself. However, its reportedly low

abundance at many locations in the Pacific islands and southeast Africa, where population growth may be hindered by the relative isolation of these populations from the closest regions of abundance, suggests that this factor may, in combination with other VP descriptors or threats, contribute to the species' extinction risk.

T. squamosina

There have been 30 documented observations of *T. squamosina* since its re-discovery in 2008, including 17 specimens from the Gulf of Aqaba and northern Red Sea, 7 individuals from the Farasan Islands in southern Saudi Arabia, and 6 individuals from an unnamed site in the southern Red Sea. The species was absent from all but 1 of the 58 survey sites visited by Rossbach *et al.* (2021) along the eastern Red Sea coast, including all sites in central and northern Saudi Arabia.

Given its exceptionally low abundance, sparse distribution, and highly restricted range, *T. squamosina* is highly susceptible to the ongoing and future threats described above, including habitat destruction and modification, continued artisanal harvest, and the inadequacy of existing regulations. Potential population reductions due to these factors threatens the persistence of remaining populations, and in effect, significantly elevates the extinction risk of *T. squamosina.* For this reason, we find that the species' low abundance puts it in danger of extinction in the near future.

Productivity

Despite exceptionally high fecundity, there is substantial evidence that low recruitment success and high mortality rates during early development lead to low productivity in most species of giant clams (Jameson, 1976; Beckvar, 1981; Fitt *et al.,* 1984; Crawford *et al.,* 1986; Munro, 1993a). Thus, as is discussed in relation to the *Abundance* risk factor above, we find it likely that all seven species are experiencing an Allee effect in locations where each species is considered rare, such that low productivity is directly correlated with low population abundance. As broadcast spawning organisms, giant clams rely on sufficient population density in order to respond to spawning cues of nearby individuals and to facilitate successful external fertilization of their gametes. The best available evidence suggests that spawning synchrony in *T. gigas* drops significantly at population densities lower than 10 ind ha–1 (Braley, 1984), and while gametes have been found to

remain viable for up to 8 hours in *T. squamosa,* viability decreases significantly with time (Neo *et al.,* 2015). It is possible that the exact distance and duration of viability may vary among species, but because reproductive success is so closely tied to population density, we find it likely that the overall effect of low abundance in reducing productivity is applicable to all seven species considered here.

For these reasons, we conclude that the low natural productivity of giant clams as well as decreased productivity due to low abundance contribute significantly to the long-term risk of extinction of all seven species. Additionally, with respect to *H. porcellanus, T. mbalavuana,* and *T. squamosina,* which are exceptionally rare throughout their ranges, we find that this factor is likely to contribute to the short-term risk of extinction in the near future.

Spatial Structure/Connectivity

As is discussed above, the best available scientific and commercial data indicate that *T. gigas* populations in the central Pacific region (*i.e.,* Kiribati, Marshall Islands, Tuvalu, and Cook Islands) are genetically differentiated from populations in the western Pacific (*i.e.,* Great Barrier Reef, Philippines, Solomon Islands, and Fiji). The same pattern is largely consistent for *T. derasa,* although there is some variability in the inferred level of connectivity between the Great Barrier Reef and the Philippines.

There is strong evidence indicating four (possibly five) genetically isolated clades (*i.e.,* groups of individuals that share similar ancestry) of *T. squamosa* in the Indo-Malay Archipelago, the northeastern Indo-Pacific (*i.e.,* northern Philippines and Cenderwasih Bay), Red Sea, and western Indian Ocean. There may be a fifth clade in the eastern Indian Ocean, but more data are needed to corroborate this finding. We could not find any data pertaining to the genetic signature of *T. squamosa* populations in the Pacific islands or on the Great Barrier Reef and therefore cannot infer the degree of connectivity to these areas.

We could not find any data regarding the genetic structure or connectivity among populations of *H. hippopus, H. porcellanus, T. mbalavuana,* or *T. squamosina.*

Based on the relatively short duration of the pelagic larval phase of giant clams (∼6–14 days), we would expect that long-range dispersal between distant locations is likely highly infrequent for each of these species, and perhaps particularly so among the regions

highlighted above (*i.e.,* the central Pacific, western Pacific, Indo-Malay Archipelago, eastern Indian Ocean, western Indian Ocean, and the Red Sea).

With respect to *T. derasa* and *T. gigas,* based on the spatial structure suggested by the available genetic data, it is unlikely that populations on the Great Barrier Reef provide significant larval subsidy to other locations of the species' ranges. Because the Great Barrier Reef represents one of the few remaining locations supporting relatively healthy populations of these species, any barrier to dispersal from this region reduces its capacity as a larval source and limits the species' rebound potential range-wide. Likewise, according to the limited genetic data, populations in Palau may function as a significant larval source only to nearby locations in the western Pacific, such as the Philippines. For this reason, based on the best available population genetic data and considering the abundance distribution of *T. derasa* and *T. gigas,* we conclude that limited connectivity, particularly between the Great Barrier Reef and other locations within the species' ranges, likely contributes significantly to the longterm extinction risk for these species, but does not in itself constitute a danger of extinction in the near future.

With respect to *T. squamosa,* the available data regarding spatial structure suggest that the relatively abundant populations in the Indo-Malay and Red Sea region likely do not provide significant larval subsidy to less abundant populations in the western Pacific and western Indian Oceans. Therefore, it is likely that the status of the populations in these regions is primarily dependent on local demographics. Reported declines of many *T. squamosa* populations in these regions due to longstanding harvest for subsistence and commercial purposes suggest that the lack of connectivity may be limiting the species' potential for population growth in these regions and exacerbating the species' extinction risk range-wide. However, because the abundance of *T. squamosa* remains relatively high in major portions of its range (*e.g.,* the Indo-Malay Archipelago, Red Sea, and Great Barrier Reef), we find it unlikely that the observed spatial structure contributes significantly to long-term or near-term risk of extinction by itself, but it may in combination with other VP descriptors or threats.

Without further information on the spatial structure and connectivity of *H. hippopus, H. porcellanus, T. mbalavuana,* and *T. squamosina,* we cannot assess the contribution of this factor to the extinction risk for these four species.

Diversity

Overall, we could find very little information regarding the genetic diversity of the seven species considered here. With respect to *T. derasa* and *T. gigas,* the best available scientific and commercial data indicate regional differences in the degree of genetic variation. Macaranas *et al.* (1992) found that mean heterozygosity of *T. derasa* based on allozyme variation was highest on the Great Barrier Reef (*h* = 0.35–0.46), intermediate in the Philippines ($h = 0.29$), and lowest in Fiji (*h* = 0.14). Similarly, Gomez *et al.* (1994) found low mean heterozygosity in both Fiji and Tonga (*h* = 0.17–0.19). While it is difficult to know the exact cause, the relatively low genetic diversity in the small island populations may be reflective of smaller populations and low rates of immigration due to their geographic remoteness. Macaranas *et al.* (1992) also note that samples from Fiji were collected from the Makogai Island hatchery, where genetic diversity may be artificially reduced. Similarly, comparing across several locations in the Indo-Pacific, Benzie and Williams (1995) found that genetic diversity of *T. gigas,* based on the percentage of polymorphic loci and mean number of alleles per locus (N_a) , was lowest in the Philippines (57.1 percent; $N_a = 2$), Marshall Islands (71.4 percent; $N_a =$ 2.3), and Kiribati (57.1 percent; $N_a =$ 2.3), and highest in the Solomon Islands $(85.7 \text{ percent}; N_a = 2.4 - 2.7)$ and the Great Barrier Reef (100 percent; $N_a =$ 2.9). Overall, while these data highlight geographic differences in the magnitude of genetic diversity in both *T. derasa* and *T. gigas,* we find no evidence to suggest that this factor contributes significantly to the extinction risk for these species by itself or in combination with other factors.

Likewise, with respect to *T. squamosa,* the best available scientific and commercial data suggest that genetic diversity in the Indo-Malay region is low relative to *T. maxima* and *T. crocea,* two other giant clam species with similarly broad distributions but which are not subject to this rulemaking. However, we find no evidence to suggest that this factor contributes significantly to the extinction risk for *T. squamosa* by itself or in combination with other factors.

With respect to *T. squamosina,* K.K. Lim *et al.* (2021) measured very low diversity of the mitochondrial DNA (*i.e.,* 16S haplotype diversity) and very few polymorphic loci, indicating that genetic diversity is very low. The authors hypothesized that the low diversity may be the result of a

population bottleneck, but cautioned that it may also reflect low natural diversity or a small sample size. In general, low genetic diversity may limit adaptive potential, and effectively lower the resilience of populations to environmental change. Thus, we have some concern that this factor may, in combination with the low abundance of the species, contribute to the long-term or near future extinction risk for *T. squamosina.*

We could not find any information regarding the genetic diversity of *H. hippopus, H. porcellanus,* or *T. mbalavuana.* Given these species' declining population trends, and the exceptionally low abundance of *H. porcellanus* and *T. mbalavuana* overall, it is possible that genetic diversity may be significantly reduced as a result of a population bottleneck. However, without any genetic testing on these species to determine diversity or effective population size, we are unable to conclude whether this is a relevant threat contributing to the species' risk of extinction.

Overall Risk Summary

Guided by the results of the demographic risk analysis and threats assessment above, we considered the best available scientific and commercial data to analyze the overall risk of extinction for each of the seven giant clam species throughout their respective ranges. We outline the conclusions and supporting rationale for each species below.

H. hippopus

Considering the best available scientific and commercial data regarding *H. hippopus* from all locations of the species' range, we determined that the most critical demographic risks to the species include the low abundance and negative trajectory of populations throughout the majority of its range, compounded by low natural productivity. Additionally, our threats assessment revealed that the past and present overutilization and associated inadequacy of existing regulatory mechanisms to address overutilization (*e.g.,* subsistence fisheries, domestic markets, and international trade in giant clam shells and shell-craft) contribute most significantly to the extinction risk of this species. Continued harvest of *H. hippopus* primarily for subsistence purposes, combined with the species' low productivity will likely drive further population declines and prevent any substantial population increases.

The best available scientific and commercial data indicate that very few abundant populations of *H. hippopus*

remain, and that in almost every location outside of Australia, domestic harvest of *H. hippopus* is ongoing. In Palau, Vanuatu, and the Marshall Islands, which are three of the five locations where we consider *H. hippopus* to be frequent, anecdotal reports indicate that harvest for subsistence and for sale in domestic markets is still very common. In Vanuatu and the Marshall Islands, there is evidence that this has significantly reduced *H. hippopus* abundance in the areas around human population centers, leaving very few remote areas with relatively healthy populations. There is very little quantitative information regarding the abundance of *H. hippopus* on the Great Barrier Reef, but anecdotal reports commonly suggest that populations of giant clams in general are healthy. There is also quantitative evidence that *H. hippopus* occurs in significant numbers in the outlying islands of NW Australia (Richards *et al.,* 2009; Skewes *et al.,* 1999), likely benefitting from the strong regulatory protections within Australian waters. Additionally, in Palau, although subsistence harvest of giant clams is permitted and is reported to occur commonly, a recent survey indicated relatively large populations of *H. hippopus* (Rehm *et al.,* 2022). As is discussed below in the Protective Efforts section, it is possible that the significant output of cultured giant clams from the Palau Mariculture Demonstration Center (PMDC) mariculture facility and reported efforts to use a portion of *H. hippopus* seedstock to enhance depleted populations in certain conservation areas may be offsetting the harvest pressure in Palau. However, without further information, we are not able to assess with confidence whether populations in Palau are stable, or whether they may be increasing or decreasing significantly due to one factor outweighing the other.

In contrast to these 5 locations where *H. hippopus* populations are relatively healthy (*i.e.,* the Great Barrier Reef, NW Australia, Palau, and remote areas of Vanuatu and the Marshall Islands), the best available scientific and commercial data indicate that, at the 21 other locations across the range with documented occurrences of this species, extensive exploitation for past commercial harvest for the shell and shell-craft industry and ongoing subsistence harvest have driven *H. hippopus* to low abundance, and in some cases, extirpation. The continued threat of overutilization and the demographic risks outlined above likely put the species at a high level of

extinction risk in these locations in the foreseeable future. However, because *H. hippopus* populations in Australia and Palau, and certain areas of Vanuatu and the Marshall Islands are relatively abundant, and the enforcement of strict harvest bans have effectively minimized the threat of overutilization in Australian waters, we cannot conclude that the species is at moderate or high risk of extinction throughout its entire range.

Significant Portion of Its Range (SPR) Analysis: H. hippopus

Under the ESA and our implementing regulations, a species may warrant listing if it is in danger of extinction or likely to become so within the foreseeable future throughout all or a significant portion of its range. Thus, a species may be endangered or threatened throughout all of its range, or a species may be endangered or threatened throughout only a significant portion of its range. Having determined that *H. hippopus* is not at moderate or high risk of extinction throughout all of its range, in order to inform the listing determination, we conducted an additional analysis to assess whether the species is at higher risk of extinction in a ''significant portion of its range'' that is, we assessed whether there is any portion of the species' range for which it is true that both (1) the portion is significant and (2) the species, in that portion, is in danger of extinction or likely to become so in the foreseeable future. A joint USFWS–NMFS policy, finalized in 2014, provided the agencies' interpretation of this phrase (''SPR Policy,'' 79 FR 37578, July 1, 2014) and explains that, depending on the case, it might be more efficient for us to address the ''significance'' question or the ''status'' question first. (Certain aspects of the SPR Policy have been invalidated by courts; we describe below where those decisions affect the SPR analysis.) Regardless of which question we choose to address first, if we reach a negative answer with respect to the first question, we do not need to evaluate the other question for that portion of the species' range.

Because there are infinite ways in which a range could be theoretically divided for purposes of this analysis, we first evaluated whether there are portions of the range of *H. hippopus* that have a reasonable likelihood of being both in danger of extinction or likely to become so in the foreseeable future, and biologically significant to the species. In other words, unless portions met both of these conditions, they were not further considered in this analysis. As discussed in the SPR Policy, as a

practical matter, a key part of this analysis is considering whether threats are geographically concentrated in some way. In this case, because we determined that the most significant threats to the species are overutilization and inadequacy of regulatory mechanisms to address overutilization, we focused our analysis on the portion of the range where these threats are most severe.

As has been discussed previously, several sources indicate that the early adoption of strict harvest prohibitions in Australia has been largely effective at preventing illegal harvest and minimizing the risk of overutilization of giant clams in Australian waters. This differs considerably from reports from every other location throughout the species' range, which consistently indicate that the threat of overutilization in combination with inadequate regulatory mechanisms to address this overutilization poses a significant extinction risk to *H. hippopus.* Thus, for the purpose of this SPR analysis, we distinguish locations in Australia (*i.e.,* the Great Barrier Reef and NW Australia) from all other locations where *H. hippopus* occurs and consider them as two separate portions of the species' range.

The portion of the range outside of Australia includes 24 countries and territories where the primary threat to the species is overutilization. In 21 of these locations (Andaman and Nicobar Islands (India), Japan, Taiwan, South China Sea, Indonesia, Malaysia, Myanmar, Philippines, Singapore, Fiji, New Caledonia, Papua New Guinea, Solomon Islands, FSM, Guam, Republic of Kiribati, CNMI, American Samoa, Samoa, Tonga, and Tuvalu), the best available scientific and commercial data, consisting of surveys as well as qualitative descriptions of abundance, suggest that past commercial harvest for the shell and shell-craft trade (primarily in the South Asia region), as well as past and ongoing subsistence harvest throughout this entire portion of the species' range has driven *H. hippopus* to low abundance, and in several cases, extirpation.

There are three main exceptions to this trend—Vanuatu, the Marshall Islands, and Palau. In Vanuatu, a single survey in 1988 spanning 13 islands reported that *H. hippopus* was ''overfished on inhabited islands but secure on two remote reefs'' (Zann & Ayling, 1988). We are not aware of any follow-up surveys, and the current status of these remote reef populations is unknown. Available reports from the Marshall Islands suggest that *H. hippopus* is relatively abundant at three

less-populated atolls, reporting ''huge undisturbed'' populations in Bok-ak and Pikaar Atolls in particular, but do not provide any quantitative data (Maragos, 1994; Beger *et al.,* 2008). Lastly, in Palau, a recent survey of the main island group and past surveys of a remote uninhabited atoll indicate that abundance of *H. hippopus* is relatively high (Rehm *et al.,* 2022). It is also important to note that, while we consider the overall abundance of *H. hippopus* in the Philippines and Indonesia to be ''rare,'' there are a number of studies reporting small areas within each country where *H. hippopus* still occurs at relatively high frequency. This includes, for example, Carbin Reef and Tubbataha Reefs Natural Park in the Philippines, and Raja Ampat and Kei Islands in Indonesia, where recently estimated population densities are over 20 ind ha–1 (Dolorosa, 2010; Lebata-Ramos *et al.,* 2010; Wakum *et al.,* 2017; Triandiza *et al.,* 2019).

However, in each of Vanuatu, the Marshall Islands, and Palau, existing regulations do not prohibit the domestic harvest of giant clams for subsistence purposes or for sale in local markets. According to Neo *et al.* (2017), giant clams, and especially *H. hippopus,* are still a prized subsistence food on most islands in Vanuatu. The same is true in Palau, where the harvest of *H. hippopus* is still very common near populated areas (L. Rehm, pers. comm., May 26, 2022), and in the Marshall Islands, where available information indicates that *H. hippopus* has historically been sold in local markets (S. Wells, 1997). Thus, while the current status of *H. hippopus* in these locations may be healthier than many other locations throughout the species' range, the threat of domestic harvest and inadequate regulatory mechanisms to address overutilization continues to expose the species to an elevated extinction risk in the foreseeable future. It seems that the principal factor protecting *H. hippopus* in Vanuatu and the Marshall Islands is simply the remoteness of the populations rather than any formal regulatory mechanism.

Theoretically, mariculture operations in Palau could potentially prevent the species from going extinct in the foreseeable future. As noted above, however, we are not able to assess whether populations in Palau are stable or are increasing or decreasing significantly due to the output of cultured giant clams compared to ongoing harvest. We did not base our assessment on the past success of mariculture operations, because of its reliance on a number of unpredictable factors (*e.g.,* funding, management

priorities, natural disasters, *etc.*). Thus, it is difficult to extrapolate the effect of mariculture beyond the next few years.

Basing our assessment on the demographic risks of low abundance and low productivity in 21 of 24 locations where the species naturally occurs, and the ongoing threats of overutilization and inadequate regulatory mechanisms to address it in all 24 locations, we conclude that in the portion of the species' range defined as all locations outside of Australia, *H. hippopus* is at moderate risk of extinction. Because the species still occurs in 24 locations within this portion of its range, which encompass a broad geographic area and variety of environmental conditions, and relatively healthy populations can still be found in the Marshall Islands, Palau, Vanuatu, and a number of small areas within the Philippines and Indonesia, we do not find that *H. hippopus* is at or near a level of abundance that places its continued persistence in question. However, given the ongoing threats of overutilization and inadequate regulatory mechanisms to address it, as well as documented populations declines that have been attributed to these threats, we find that the species is on a trajectory that puts it at a high level of extinction risk within the foreseeable future in the portion consisting of 24 countries and territories outside of Australia.

Having reached a positive answer with respect to the ''status'' question, we move on to determine whether this portion of the range is ''significant.'' The definition of ''significant'' in the SPR Policy has been invalidated in two District Court cases that addressed listing decisions made by the USFWS. The SPR Policy set out a biologicallybased definition that examined the contributions of the members in the portion to the species as a whole, and established a specific threshold (*i.e.,* when the loss of the members in the portion would cause the overall species to become threatened or endangered). The courts invalidated the threshold component of the definition because it set too high a standard. Specifically, the courts held that, under the threshold in the policy, a species would never be listed based on the status of the species in the portion, because in order for a portion to meet the threshold, the species would be threatened or endangered range-wide. See *Center for Biological Diversity* v. *Jewell,* 248 F. Supp. 3d 946, 958 (D. Ariz. 2017); *Desert Survivors* v. *DOI,* 321 F. Supp. 3d 1011 (N.D. Cal. 2018). However, those courts did not take issue with the fundamental approach of evaluating

significance in terms of the biological significance of a particular portion of the range to the overall species. NMFS did not rely on the definition of "significant" in the policy here. Rather, to assess whether a portion of a species' range is ''significant,'' we consider relevant biological information, such as whether the portion was historically highly abundant, potentially functioning as a source population for other areas of the range, whether there is evidence that it was historically highly productive with potential to contribute to the population growth of this species as a whole, whether the portion encompasses a substantial area relative to the species' current range, whether the portion historically facilitated gene flow between populations, and whether the portion contains genetic or phenotypic diversity that is important to species viability. The contribution or role of that portion to the viability of the species as a whole is also considered from a historical, current, and future perspective to the extent possible.

With respect to *H. hippopus,* there is strong evidence that the portion of the species' range defined as all locations outside of Australia qualifies as a ''significant portion.'' Based on historical trade statistics, as well as the countless reports describing major population losses resulting from years of domestic harvest and intense commercial harvest, primarily for the international shell and shell-craft industry (*e.g.,* see Villanoy *et al.,* 1988; Kinch, 2003; Dolorosa & Schoppe, 2005; Harahap *et al.,* 2018; Purcell *et al.,* 2020), it is clear that *H. hippopus* was historically highly abundant in this portion of its range.

Furthermore, prior to these losses, it is likely that populations in this portion, which includes 24 of 26 locations comprising the species' range (*i.e.,* all locations except for the Great Barrier Reef and NW islands in Australia), played a critical role in maintaining genetic connectivity throughout the species' range. For many marine organisms, and particularly sedentary taxa such as giant clams, long-range dispersal (*e.g.,* between islands and other distant locations) is likely highly stochastic and infrequent (see Cowen *et al.,* 2003; Siegel *et al.,* 2008). As is discussed above in *Growth and Reproduction,* it relies on a process known as 'sweepstakes' reproduction, in which spawning and fertilization coincidentally align with oceanographic conditions that facilitate successful long-distance dispersal and recruitment to a suitable habitat. The relatively short pelagic larval duration of giant clams

(∼6–14 days) further limits the probability of long-distance dispersal. Thus, it is likely that *H. hippopus* was dependent on serial migration between nearby locations (*i.e.,* 'stepping stones') to maintain genetic connectivity throughout its range. Historically, this portion would have once facilitated this connectivity between populations.

Given its geographic size, this portion of the species' range encompasses a wide variety of habitats and environmental conditions. Therefore, we expect that, to some extent, past populations were likely genetically adapted to their local setting, as has been demonstrated with respect to numerous other marine organisms across similar geographic scales (*e.g.,* see Sanford & Kelly, 2011 for comprehensive review). Such genetic diversity can function as an important foundation to enhance the resilience of the species and facilitate future adaptation to environmental change. Furthermore, given the geographic extent of this portion of this range and the varied habitats it encompasses, the populations of *H. hippopus* within this portion would have provided an important demographic reserve, which could facilitate recovery following stochastic mortality events or other localized population declines.

Based on the rationale described above, we find that the portion of the species' range defined as all locations outside of Australia is ''significant,'' and serves a biologically important role in maintaining the long-term viability of *H. hippopus.*

H. porcellanus

Despite a lack of formal, comprehensive abundance estimates, the best available scientific and commercial data suggest that *H. porcellanus* has suffered significant population declines since the 1970s, leading to low abundance and very few remaining populations throughout its historical range. The inherent risks of such low abundance are compounded by low natural productivity, which likely prevents any substantial shortterm rebound. Additionally, our threats assessment revealed that past and present overutilization in subsistence fisheries, domestic markets, and the international trade of giant clam shells and shell-craft, as well as the inadequacy of existing regulatory mechanisms to address this overutilization contribute most significantly to the extinction risk of this species. *H. porcellanus* has historically been highly desired commercially for the aesthetic of its shell and once comprised a substantial

portion of the giant clam shell export volume from the Philippines, reaching a total export of nearly a million *H. porcellanus* shells and shell pairs between 1978 and 1992. While *H. porcellanus* is no longer legally exported from the Philippines, reports of ongoing subsistence harvest throughout its range and illegal poaching to supply a continued demand for giant clam shells and shell-craft throughout East Asia suggest that the species will likely continue to experience declining trends in its abundance and productivity in the foreseeable future. Based on our assessment of these threats and demographic risk factors, we conclude that *H. porcellanus* is at a high risk of extinction throughout its range.

T. derasa

Considering the best available scientific and commercial data regarding *T. derasa* from all locations of the species' range, we determined that the most critical demographic risks to *T. derasa* are the low abundance and negative trajectory of populations throughout the majority of its range, compounded by low natural productivity and the likelihood of the Allee effect. Additionally, our threats assessment revealed that the past and present overutilization due to subsistence fisheries, domestic markets, and the international trade of giant clam meat and poaching, as well as the inadequacy of existing regulatory mechanisms to address this overutilization contribute most significantly to the extinction risk of this species. Continued harvest of *T. derasa* primarily for subsistence purposes, combined with the species' low productivity will likely drive further population declines and prevent any substantial population rebound. We also consider that the close association of *T. derasa* with coral reefs may make the species more susceptible to the projected impacts of ocean warming and acidification on coral reef habitats.

As with *H. hippopus,* the best available scientific and commercial data indicate that very few abundant populations of *T. derasa* remain and occur primarily in the waters of Australia. Extensive surveys of *T. derasa* on the Great Barrier Reef from the 1980s (Braley, 1987a, 1987b) found that the species' distribution was patchy with several sites of relatively high density (>10 ind ha–1) interspersed among many other sites of low abundance or where the species was completely absent. The Swain Reefs in particular, a group of approximately 350 offshore reefs in the southern region of

the Great Barrier Reef, was one area described as having especially high abundance of *T. derasa,* with densities ranging from 12 to 172 ind ha–1 (Pearson, 1977). Based on the species' patchy distribution and the observed pattern of recruitment, Braley (1988) found it likely that the relatively few reefs with abundant populations of clams (mostly in the south) may dominate recruit production for the rest of the Great Barrier Reef.

According to Pearson (1977), during the 1960s and early 1970s, Taiwanese vessels poached giant clams (primarily *T. gigas* and *T. derasa*) from the entire length of the Great Barrier Reef. As surveillance and enforcement efforts by Australian authorities increased in the 1970s, poachers began to concentrate their activities to offshore areas, such as the Swain Reefs, but this likely only lasted at significant scale for a few years, as Dawson (1986) claimed that during the lead up to the declaration of the Australian Fishing Zone (AFZ) in 1979, Taiwanese authorities were warned that continued illegal poaching of giant clams would jeopardize Taiwan's position in gaining access rights to the AFZ. This forced the Taiwanese government to enhance inspection of suspected boats upon departure and return to port. According to Dawson (1986), ''the combined effect of these two components, almost certain apprehension by the coastal State and effective sanctions by the flag State, combined to result in the virtual cessation of illegal giant clam activities in the AFZ.'' Based on this assessment and because subsistence demand for giant clams in Australia is minimal, we find it likely that the population density estimates provided by Braley (1987a, 1987b) generally represent the current status of *T. derasa* on the Great Barrier Reef. This is further supported by more recent reviews and reports (bin Othman *et al.,* 2010; Braley, 2023; Neo *et al.,* 2017; S. Wells, 1997) suggesting that *T. derasa* is still relatively abundant on much of the Great Barrier Reef.

There is also quantitative evidence that *T. derasa* occurs in significant numbers in the outlying islands of NW Australia (Richards *et al.,* 2009; Skewes *et al.,* 1999), likely benefitting from the strong regulatory protections within Australian waters. Additionally, in Palau, although subsistence harvest of giant clams is permitted and is reported to occur commonly, a recent survey indicated relatively large populations of *T. derasa* (Rehm *et al.,* 2022). As with *H. hippopus,* it is possible that the significant output from the PMDC mariculture facility and reported efforts to use a portion of *T. derasa* seedstock

to enhance depleted populations in certain conservation areas may be balancing the harvest pressure in Palau. However, without further information, we are not able to assess with confidence whether *T. derasa* abundance in this location is stable, or whether it may be increasing or decreasing significantly due to one factor outweighing the other.

In contrast to these 3 locations where *T. derasa* populations are relatively healthy (*i.e.,* the Great Barrier Reef, NW Australia, Palau), the best available data indicate that, at the 15 other locations across the range where this species naturally occurs, extensive exploitation for past commercial trade, ongoing subsistence use, and illegal harvest have driven *T. derasa* to exceptionally low abundance, and in some cases, extirpation. The continued threat of overutilization, the inadequacy of existing regulatory mechanisms to address overutilization, the possible future threat of habitat degradation due to climate change impacts on coral reefs, and the demographic risks outlined above, likely put the species at a high level of extinction risk in these locations. However, because *T. derasa* populations in Australia and Palau are relatively abundant, and the enforcement of strict harvest bans have effectively minimized the threat of overutilization in Australian waters, we cannot conclude that the species is at moderate or high risk of extinction throughout its entire range.

It is worth highlighting that, although we refer to the Great Barrier Reef as only one location for the purpose of this analysis, it covers an expansive geographic area that comprises a substantial proportion of the suitable habitat within the species' range. Additionally, while the future threat of habitat degradation due to climate change impacts on coral reefs may be relevant to these populations, we do not have sufficient information to confidently assess the extent to which the survival or productivity of giant clams (even those species closely associated with coral reefs, such as *T. derasa*) may be impacted by projected changes to coral reef communities.

SPR Analysis: T. derasa

Having determined that *T. derasa* is not at moderate or high risk of extinction throughout all of its range, in order to inform the listing determination, we conducted an additional analysis to assess whether the species is at higher risk of extinction in a ''significant portion of its range'' that is, we assessed whether there is any portion of the species' range for which

it is true that both (1) the portion is significant and (2) the species, in that portion, is in danger of extinction or likely to become so in the foreseeable future.

Because we determined that the most significant threats to *T. derasa* are overutilization and the inadequacy of regulatory mechanisms to address overutilization, we focused our analysis on the portion of the range where these threats are most severe, consistent with the approach used in the SPR analysis for *H. hippopus.* As discussed above, several sources indicate that the early adoption of strict harvest prohibitions in Australia has been largely effective at preventing illegal harvest and minimizing the risk of overutilization of giant clams in Australian waters. This differs considerably from reports from every other location throughout the species' range, which consistently indicate that the threat of overutilization in combination with inadequate regulation and enforcement poses a significant extinction risk to *T. derasa.* Thus, for the purpose of this SPR analysis, we distinguish locations in Australia (*i.e.,* the Great Barrier Reef and NW Australia) from all other locations where *T. derasa* occurs and consider them as two separate portions of the species' range.

In this case, the portion outside of Australia that was further considered includes 16 countries and territories (Christmas Island, Cocos (Keeling) Islands, Taiwan, South China Sea, Indonesia, Malaysia, Philippines, Fiji, New Caledonia, Papua New Guinea, Solomon Islands, Vanuatu, Guam, CNMI, Palau, and Tonga) where the primary threat to the species is overutilization. In 15 of these locations, the best available scientific and commercial data, consisting of surveys as well as qualitative descriptions of abundance, suggest that past commercial harvest for the giant clam meat trade, past and ongoing subsistence harvest, and widespread illegal poaching have driven *T. derasa* to exceptionally low abundance, and in several cases, extirpation. The one exception is Palau, where a recent survey of the main island group and past surveys of a remote uninhabited atoll indicate that abundance of *T. derasa* is likely relatively high. However, as is discussed above, while commercial export of wild-caught giant clams is prohibited in Palau, harvest for subsistence purposes and for sale in domestic markets is reportedly very common, and *T. derasa* is one species that is specifically targeted by locals.

As with *H. hippopus,* the success of mariculture operations in Palau could theoretically prevent the species from going extinct in the foreseeable future. For example, since 1990, the PMDC alone has cultured over 150,000 *T. derasa* for export internationally, and likely many more that were traded or distributed domestically, or were otherwise not included in CITES reports. It is possible that the threat of overutilization in Palau has been somewhat offset in the short term by documented efforts to reseed depleted populations (see Protective Efforts). However, as we discussed previously with respect to *H. hippopus,* we are not basing our assessment on the past success of mariculture operations; its reliance on a number of unpredictable factors (*e.g.,* funding, management priorities, natural disasters, *etc.*) makes it difficult to extrapolate the effect of mariculture beyond the next few years. Thus, we based our assessment on the demographic risks of low abundance and low productivity that exist in 15 of 16 locations in this portion where the species naturally occurs, and the ongoing threats of overutilization and inadequate regulatory mechanisms to address it in all 16 locations.

Similar to *H. hippopus,* we considered the geographic range of the remaining populations, noting that the species still occurs in 16 locations within this portion of its range, which encompass a broad geographic area and a variety of environmental conditions within the Indo-Pacific region. However, Palau is the only location in this portion where *T. derasa* is considered frequent (although, we note that two recent surveys have found relatively abundant populations in the Anambas Islands and Raja Ampat region of Indonesia). Because of its large size, *T. derasa* is often the most highly desired species for subsistence consumption and to sell for its meat in local markets. This continued demand at the local level, combined with the widespread and lasting impact of the Taiwanese poaching effort, has driven the species to exceptionally low abundance on average in this portion of its range. Among the many low estimates of population density, *T. derasa* has been described as ''virtually extinct from most of [the Philippines] due to overexploitation'' (Gomez & Alcala, 1988), ''likely functionally extinct'' from Karimun Jawa, Indonesia (Brown & Muskanofola, 1985), and ''at risk of extirpation'' in New Caledonia (Purcell *et al.,* 2020). For these reasons, despite the geographic scope of the remaining *T. derasa* populations, given the desirability and ongoing demand for *T. derasa* for consumption and sale in

local markets, we find that the species is at or near a level of abundance that places its continued persistence in this portion in question (high extinction risk).

Having reached a positive answer with respect to the ''status'' question, we next considered whether this portion of the range is ''significant.'' Similar to the SPR analysis for *H. hippopus,* we considered the historically high abundance of *T. derasa* in this portion of the range, as evidenced by trade statistics and the many reports of major population losses resulting from years of subsistence and commercial harvest. Additionally, as was described with respect to *H. hippopus,* it is likely that populations in this portion played an important role in maintaining genetic connectivity throughout the species' range. Given the relatively short pelagic larval phase of giant clams (∼6–14 days), there is a diminishing likelihood of larval dispersal between locations at progressively greater distances. Therefore, genetic exchange between distant populations likely relied on many smaller dispersal events across the network of more closely spaced islands or habitat areas that comprise this portion of the species' range. Lastly, considering the geographic extent of this portion and the diverse habitats that it encompasses, the populations of *T. derasa* within this portion likely served as an important demographic and genetic reserve, which could facilitate recovery following localized population declines. Based on this rationale, we find that the portion of the species' range defined as all locations outside of Australia is ''significant,'' or in other words serves a biologically important role in maintaining the long-term viability of *T. derasa.*

T. gigas

Considering the best available scientific and commercial data regarding *T. gigas* from all locations of the species' range, we determined that the most critical demographic risks to *T. gigas* are the low abundance and negative trajectory of populations throughout the majority of its range, compounded by low natural productivity and likely Allee effect. Additionally, our threats assessment revealed that the past and present overutilization due to subsistence fisheries, domestic markets, the international trade of giant clam meat and poaching, and the international trade of giant clam shells and shell-craft, as well as the inadequacy of existing regulatory mechanisms to address this overutilization contribute most significantly to the extinction risk of

this species. Continued harvest of *T. gigas* primarily for subsistence purposes and illegally by poachers, combined with the species' low productivity will likely drive further population declines and prevent any substantial population recovery in locations where it is rare.

The best available scientific and commercial data indicate that very few abundant populations of *T. gigas* remain and occur exclusively on the Great Barrier Reef in Australia. Extensive surveys of *T. gigas* on the Great Barrier Reef from the 1980s (Braley, 1987a, 1987b) recorded population densities as high as 56 ind ha⁻¹, with numerous sites hosting populations of *T. gigas* at densities greater than 10 ind ha–1 interspersed among other sites of low abundance or where the species was completely absent. Braley (1987a) noted that *T. gigas* was present on 36 of 57 (63 percent) randomly chosen survey sites, and 17 of 19 (89 percent) sites chosen specifically because of known giant clam populations. High population densities were found in the Cairns, Cooktown, and Escape Reefs transects, while no living *T. gigas* were observed south of 19° S. Based on the species' patchy distribution and the observed pattern of recruitment, Braley (1988) found it likely that the scattered reefs hosting abundant populations of clams (mostly in the south) may dominate recruit production for the rest of the Great Barrier Reef.

As was discussed in the extinction risk analysis for *T. derasa,* Taiwanese vessels poached giant clams (primarily *T. derasa* and *T. gigas*) from the Great Barrier Reef during the 1960s and 1970s. However, strict enforcement of a harvest ban on giant clams resulted in the virtual cessation of illegal giant clam activities in Australia by the mid-1980s. Based on this information and because giant clams are not harvested for subsistence in Australia, we find it likely that the population density estimates provided by Braley (1987a, 1987b) generally represent the current status of *T. gigas* on the Great Barrier Reef. This is further supported by more recent reviews and reports (bin Othman *et al.,* 2010; Braley, 2023; Neo *et al.,* 2017; S. Wells, 1997) suggesting that *T. gigas* is still relatively abundant on much of the Great Barrier Reef. According to R.D. Braley (pers. comm., October 19, 2022) and Neo *et al.* (2017), the distribution of *T. gigas* on the Great Barrier Reef represents a ''natural'' and ''virtually undisturbed'' state for the species.

In contrast to the Great Barrier Reef, where *T. gigas* populations are relatively healthy, the best available data indicate that, at the other 32 of 33 locations across the range with documented natural occurrence of this species, extensive exploitation for past commercial trade, ongoing subsistence use, and illegal harvest have driven *T. gigas* to exceptionally low abundance, and in many cases, extirpation (this applies to all locations except NW Australia, where the low abundance cannot be attributed to harvest). The continued threat of overutilization, the possible future threat of habitat degradation due to climate change impacts on coral reefs, and the demographic risks outlined above, places the continued persistence of *T. gigas* in these locations in question. However, because *T. gigas* populations on the Great Barrier Reef are relatively abundant, even described as ''virtually untouched,'' and the enforcement of strict harvest bans have effectively minimized the threat of overutilization in Australian waters, we cannot conclude that the species is at moderate or high risk of extinction throughout its entire range.

It is worth highlighting that, although we refer to the Great Barrier Reef as only one location for the purpose of this analysis, it covers an expansive geographic area that comprises a substantial proportion of the suitable habitat within the species' range. Additionally, as is mentioned in regard to *T. derasa,* while the future threat of habitat degradation due to climate change impacts on coral reefs may be relevant to *T. gigas* populations, including those on the Great Barrier Reef, we do not have sufficient information to confidently assess the extent to which the survival or productivity of giant clams may be impacted by projected changes to coral reef communities.

SPR Analysis: T. gigas

Having determined that *T. gigas* is not at moderate or high risk of extinction throughout all of its range, in order to inform the listing determination, we conducted an additional analysis to assess whether the species is at higher risk of extinction in a ''significant portion of its range''—that is, we assessed whether there is any portion of the species' range for which it is true that both (1) the portion is significant and (2) the species, in that portion, is in danger of extinction or likely to become so in the foreseeable future.

Because we determined that the most significant threats to *T. gigas* are overutilization and the inadequacy of regulatory mechanisms to address overutilization, we focused our analysis on the portion of the range where these threats are most severe, consistent with

the approach used for both *H. hippopus* and *T. derasa.* As has been discussed, several sources indicate that the early adoption of strict harvest prohibitions in Australia has been largely effective at preventing illegal harvest and minimizing the risk of overutilization of giant clams in Australian waters. This differs considerably from reports from every other location throughout the species' range, which consistently indicate that the threat of overutilization in combination with inadequate regulatory mechanisms to address that threat pose a significant extinction risk to *T. gigas.* Thus, for the purpose of this SPR analysis, we distinguish locations in Australia (*i.e.,* the Great Barrier Reef and NW Australia) from all other locations where *T. gigas* occurs and consider them as two separate portions of the species' range.

In this case, the portion of the range outside of Australia that we considered further includes 29 countries and territories (Andaman and Nicobar Islands (India), Christmas Island, Cocos (Keeling) Islands, Japan, Taiwan, China, South China Sea, Indonesia, Malaysia, Myanmar, Cambodia, Philippines, Singapore, Thailand, Vietnam, East Timor, Fiji, New Caledonia, Papua New Guinea, Solomon Islands, Vanuatu, FSM, Guam, Republic of Kiribati, Marshall Islands, CNMI, Palau, Tonga, and Tuvalu) where the primary threat to the species is overutilization. In all of these locations, the best available scientific and commercial data, consisting of survey data as well as qualitative descriptions of abundance, suggest that past commercial harvest for the giant clam meat trade, past and ongoing subsistence harvest, and widespread illegal poaching have driven *T. gigas* to exceptionally low abundance, and in many cases, extirpation. Based on the demographic risks of low abundance and low productivity in this portion, and the ongoing threats of overutilization and inadequate regulatory mechanisms to address overutilization in all 29 locations, we conclude that in the portion of the species' range defined as all locations outside of Australia, *T. gigas* is at or near a level of abundance that places it at high risk of extinction.

To evaluate whether this portion is ''significant,'' we applied similar rationale as was used with respect to the SPR analyses for *H. hippopus* and *T. derasa.* We considered the historically high abundance of *T. gigas* in this portion of the range, as evidenced by trade statistics and the many reports of major population losses resulting from years of subsistence and commercial harvest. Additionally, as was described

in relation to *H. hippopus* and *T. derasa,* it is likely that populations of *T. gigas* in this portion played an important role in maintaining genetic connectivity throughout the species' range. Given the relatively short pelagic larval phase of giant clams (∼6–14 days), there is a diminishing likelihood of larval dispersal between locations at progressively greater distances. Therefore, genetic exchange between distant populations likely relied on many smaller dispersal events across the network of more closely spaced islands or habitat areas that comprise this portion of the species' range. Lastly, considering the geographic extent of this portion and the diverse habitats that it encompasses, the populations of *T. gigas* within this portion likely served as an important demographic and genetic reserve, which could facilitate recovery following localized population declines. Based on this rationale, we find that the portion of the species' range defined as all locations outside of Australia is ''significant,'' or in other words serves a biologically important role in maintaining the long-term viability of *T. gigas.*

T. mbalavuana

Despite a lack of formal, comprehensive abundance estimates, the best available scientific and commercial data suggest that *T. mbalavuana* occurs at exceptionally low abundance and is sparsely distributed throughout its highly restricted range. Anecdotal accounts from traditional fishermen in Tonga indicate that the species has experienced significant population loss since the 1940s, which has been attributed at least in part to longstanding harvest of giant clams in both Fiji and Tonga, where the species primarily occurs. The inherent risks of such low abundance are compounded by low natural productivity and the likelihood of the Allee effect, which likely prevents any substantial shortterm recovery. Additionally, our threats assessment revealed that past and present overutilization and associated inadequacy of existing regulatory mechanisms at the local level contribute most significantly to the extinction risk of this species. *T. mbalavuana* has historically been and continues to be collected for subsistence consumption and for sale in domestic markets, occasionally being mistaken for *T. derasa* by local fishermen. While commercial export of giant clams has been prohibited in both Fiji and Tonga, existing regulations afford little protection to the species from the ongoing domestic harvest. Based on our assessment of these threats and

demographic risk factors, we conclude that *T. mbalavuana* is at a high risk of extinction throughout its range.

T. squamosa

Considering the best available scientific and commercial data regarding *T. squamosa* from all locations of the species' range, we determined that the most critical demographic risk to the species is the low natural productivity of giant clams generally, reflected by reports of little to no *T. squamosa* recruitment in several recently published surveys from Malaysia, Singapore, and Palau. Additionally, our threats assessment revealed that past and present overutilization due to subsistence fisheries, domestic markets, the international trade of giant clam shells and shell-craft, and the international trade of live giant clams for aquaria, as well as the inadequacy of existing regulatory mechanisms to address overutilization contribute most significantly to the extinction risk of this species. Continued harvest of *T. squamosa* primarily for subsistence purposes, combined with the species' low productivity may drive further population declines and prevent substantial recovery in locations where the species is already rare, including much of southeast Africa and the Pacific islands.

However, the best available scientific and commercial data indicate that there are a number of locations where *T. squamosa* still occurs at relatively high abundance. This includes significant portions of South Asia and the Red Sea, two regions which notably have been subjected to a long history of subsistence harvest, and in the case of South Asia, intense commercial trade of *T. squamosa* shells throughout the 1980s. Yet, based on available reports, we consider *T. squamosa* to be ''frequent'' (10–100 ind ha–1) or ''abundant'' (>100 ind ha–1) in locations such as Indonesia, the Philippines, Malaysia, Australia (Great Barrier Reef), the Solomon Islands, and Saudi Arabia, all of which host substantial coral reef habitat, and likely also suitable habitat for *T. squamosa* based on the species' known habitat preferences. Furthermore, of the 63 locations where *T. squamosa* has been observed, it has been reported as likely extirpated in only 2 of them. Thus, its current distribution encompasses an expansive geographic range and broad array of environmental conditions. Together, these factors suggest that, despite the many reports of population decline in most locations throughout its range, *T. squamosa* may be somewhat resilient to

the threat of subsistence harvest at its current level, particularly in the Indo-Malay and Red Sea regions.

The general lack of information regarding *T. squamosa* productivity (*e.g.,* natural reproductive and recruitment success) and long-term abundance trends limits our understanding of the factors that may underlie this apparent resilience. One important factor may be that, although *T. squamosa* was harvested extensively for the commercial shell trade in the 1980s, it was not targeted for its meat by commercial entities and illegal poachers with the same intensity as *T. gigas* and *T. derasa,* which severely depleted these species in the South Asia region. It is also possible that the global abundance of *T. squamosa* was historically larger than other giant clam species, or that high demographic connectivity within the Indo-Pacific and Red Sea regions, as is suggested by the available population genetic data, may facilitate significant larval exchange and recovery of depleted populations.

Regardless, given the relatively high abundance of *T. squamosa* in major portions of its range and its expansive distribution, we conclude that the species is at low risk of extinction throughout its entire range. In other words, based on the best available scientific and commercial data, we find it unlikely that the current and projected threats to the species, namely ongoing subsistence harvest and inadequate regulatory mechanisms to address overutilization, place the continued existence of *T. squamosa* in question presently or within the foreseeable future.

SPR Analysis: T. squamosa

Having determined that *T. squamosa* is at low risk of extinction throughout all of its range, in order to inform the listing determination, we conducted an additional analysis to assess whether the species is at higher risk of extinction in a ''significant portion of its range'' that is, we assessed whether there is any portion of the species' range for which it is true that both (1) the portion is significant and (2) the species, in that portion, is in danger of extinction or likely to become so in the foreseeable future. We analyzed two different configurations of portions (*e.g.,* Australia and all areas where *T. squamosa* currently is known to occur outside of Australia; and Red Sea, southeast Africa, Indo-Malay Archipelago, and Cenderwasih Bay), both of which had a reasonable likelihood of meeting these conditions, as described in more detail below.

As with the SPR analyses for *H. hippopus, T. derasa,* and *T. gigas,* because we determined that the most significant threats to *T. squamosa* are overutilization and inadequacy of regulatory mechanisms to address that threat, we base our analysis here on the portion of the range where these threats are most severe. Using the same rationale as was used for *H. hippopus, T. derasa,* and *T. gigas,* we distinguish locations in Australia (*i.e.,* the Great Barrier Reef and NW Australia) from all other locations where *T. squamosa* occurs and consider them as two separate portions of the species' range.

The portion outside of Australia that we further considered includes 59 countries and territories (see table 1) where the primary threat to the species is overutilization due to subsistence fisheries, domestic markets, the international trade of giant clam shells and shell-craft, and the international trade of live giant clams for aquaria. Unlike the SPR analyses for *H. hippopus, T. derasa,* and *T. gigas,* however, there are a number of locations, including the Philippines, Indonesia, Malaysia, and much of the Red Sea, where the best available scientific and commercial data suggest that *T. squamosa* abundance is quite high and where there is substantial coral reef area, and likely suitable habitat for *T. squamosa* based on the species' known habitat preferences.

While it is clear that *T. squamosa* has suffered significant population declines throughout much of this portion of its range, available reports suggest that a major fraction of the loss can be attributed to the intense commercial demand for its shell and shell products in the 1980s, particularly in the South Asia region. Since the early 1990s, when the commercial shell industry in the Philippines began to dwindle, harvest of *T. squamosa* has primarily been limited to a smaller scale, mostly for subsistence consumption or for sale in local markets. As is discussed above, harvest for subsistence purposes continues to occur in all locations outside of Australia, constituting the most significant present and future threat to *T. squamosa* within this portion of its range.

Without the benefit of long-term monitoring data, we are not able to assess population trends over the last few decades to quantitatively evaluate the effect of the ongoing subsistence harvest. However, given the reports of relatively high abundance in locations such as the Philippines, Indonesia, and Malaysia, where *T. squamosa* has been subjected to both commercial harvest and longstanding subsistence harvest,

and much of the Red Sea, where subsistence harvest is common, we find that *T. squamosa* is at low risk of extinction in this portion of its range.

Having determined that *T. squamosa* is at low risk of extinction in the portion of its range including all locations outside of Australia, we also considered population genetics as a means of delineating alternative portions of the species' range. As is discussed above, the best available population genetic data indicate at least four (possibly five) discrete metapopulations, located in the Red Sea, southeast Africa, Indo-Malay Archipelago, and Cenderwasih Bay in northern Papua (and a possible fifth population in the eastern Indian Ocean). Studies of other broadly distributed species (*e.g., T. maxima* and *T. crocea*) suggest that there may also be genetic breaks between the central and western Pacific islands, and also between the western Pacific and Indo-Malay Archipelago (Nuryanto & Kochzius, 2009; Huelsken *et al.,* 2013; Hui *et al.,* 2016). However, we were not able to find any studies including data from *T. squamosa* populations in the Pacific islands to confirm these patterns in this species. Because population genetic patterns are often variable between species, we cannot rely on these inferences for the purposes of this analysis.

Therefore, we consider the populations of *T. squamosa* in the Red Sea, southeast Africa, Indo-Malay Archipelago, and Cenderwasih Bay as four distinct portions of the species' range. As has been addressed above, the relatively high abundance of *T. squamosa* within the Red Sea and Indo-Malay regions leads us to conclude that the species is likely at low risk of extinction in these portions of its range. With respect to the portions in southeast Africa and in Cenderwasih Bay, given their genetic and likely demographic isolation from the majority of the species' range, as well as the relatively small geographic area they occupy, we do not find that these two portions can be considered ''significant,'' or that they likely serve a biologically important role in maintaining the long-term viability of this species. Thus, as a result of this SPR analysis, we do not find any portions within the range of *T. squamosa* for which it is true that both the portion is significant and that the species in the portion is at moderate or high risk of extinction.

T. squamosina

The best available scientific and commercial data suggest that *T. squamosina* occurs at exceptionally low abundance and is sparsely distributed

throughout its highly restricted range. Since the re-discovery of the species in 2008, there have been only 30 recorded observations of *T. squamosina,* which are divided between the Gulf of Aqaba in the northern Red Sea and two sites including the Farasan Islands in the south. The inherent risks of such low abundance are compounded by low natural productivity, which likely prevents any substantial recovery of the species in the near future. Additionally, our threats assessment revealed that past and present overutilization and associated inadequacy of existing regulatory mechanisms at the local level contribute most significantly to the extinction risk of this species. *T. squamosina* has historically been and continues to be collected for subsistence consumption and for sale in domestic markets, and the existing regulatory mechanisms are limited to the management of a few protected areas, affording little protection to the species in the remainder of its range. Based on our assessment of these threats and demographic risk factors, we conclude that *T. squamosina* is at a high risk of extinction throughout its range.

Protective Efforts

Section 4(b)(1)(A) of the ESA requires that NMFS make listing determinations based solely on the best available scientific and commercial data after conducting a review of the status of the species and taking into account those efforts, if any, being made by any State or foreign nation, or political subdivisions thereof, to protect and conserve the species. Above, we identified local and international regulatory mechanisms that have been adopted in some parts of these species' ranges, and determined that these mechanisms were generally inadequate to address threats arising from overutilization outside of Australia. In reaction to dwindling giant clam stocks throughout the Indo-Pacific, several nations have supported efforts exploring the use of mariculture to replenish and/ or re-establish populations in local waters. As of 2016, there were an estimated 20 giant clam mariculture facilities in operation, primarily in the Pacific islands, as well as in Indonesia, Malaysia, the Philippines, and Australia (Mies, Dor, *et al.,* 2017). Here, we specifically examine whether mariculture efforts may be contributing to the protection and conservation of the seven giant clam species at issue in this proposed rulemaking.

There is extensive literature highlighting the challenges of giant clam mariculture generally, and particularly for the purpose of stock replenishment

(Munro, 1993a; Gomez & Mingoa-Licuanan, 2006; Teitelbaum & Friedman, 2008; Mies, Scozzafave, *et al.,* 2017). The primary barrier to these efforts is the exceptionally low survival rate of giant clam larvae postfertilization compounded by the time and resources required to protect juveniles once they have been outplanted and before they reach a size at which they are sufficiently protected from predation. Despite the numerous restocking and translocation programs known to exist throughout the Indo-Pacific, most are reported to still be operating on a small or pilot scale with only partial success, and further intensification of giant clam mariculture for the purpose of stock replenishment or reintroduction is in most cases considered economically unviable (Teitelbaum & Friedman, 2008; UNEP– WCMC, 2012).

One possible exception is in Palau, where the PMDC has pioneered many of the methods for giant clam mariculture and has successfully cultured large numbers of giant clams, particularly *T. derasa.* Following receipt of funding from the United States in 1982, the PMDC expanded production of giant clams substantially, and the facility began exporting significant quantities of ''seed'' clams (*i.e.,* small juveniles) and broodstock to many other Indo-Pacific countries and territories (Shang *et al.,* 1994). It is difficult in most cases to determine the exact purpose of the shipments—some were intended to be used exclusively for conservationrelated stock enhancement, while others were used to establish local hatcheries for the purpose of subsistence or commercial harvest. Additionally, there are reports that a portion of the *H. hippopus* and *T. derasa* culture stock is being used to enhance giant clam populations in 23 conservation areas around Palau (Kinch & Teitelbaum, 2010; L. Rehm, pers. comm., May 26, 2022). We could not find any follow-up surveys specifically documenting the success of these efforts (or lack thereof). According to L. Rehm (pers. comm., May 26, 2022), authorities in Palau struggle to enforce the regulations of conservation areas, particularly those on offshore reefs, because they lack sufficient personnel and equipment, potentially negating any benefit of reseeding.

In regard to the individual species addressed here, several countries are known to have imported *H. hippopus* broodstock for the purposes of stock enhancement or reintroduction, but there is very little information regarding the success of these efforts in establishing sustainable populations of

H. hippopus in the wild. An unpublished report by Braley (*n.d.*) describes the outcome of translocating a single cohort of *H. hippopus* (∼70,000 specimens) from Australia to Fiji, Tonga, and the Cook Islands in 1991. According to the report, survival to mid-1997 averaged 1.79 percent across all the countries, and was considerably higher in Tonga (5.2 percent) compared to Fiji (0.04 percent) and the Cook Islands (0.13 percent). In Fiji and the Cook Islands, only 9 and 27 clams, respectively, remained in 1997 from the original 25,000 and 20,000 clams delivered to the countries in 1991. In Tonga, 1,300 of the 25,000 original clams survived to 1997, but many of these were still being actively managed in protective cages on the sand flat.

There have also been a number of countries and territories which have cultured or imported *T. derasa* and *T. gigas* for the purpose of restocking depleted populations or to introduce the species to locations outside of its natural range. Because of its relatively fast growth rate, *T. derasa* has been a priority for mariculture throughout the Indo-Pacific for many years. There are at least 17 countries and territories with hatchery and/or growout facilities that have cultured *T. derasa* for the purpose of enhancing depleted populations (Lindsay *et al.,* 2004; Mies, Dor, *et al.,* 2017), and several others that have initiated *T. derasa* restocking programs without domestic hatcheries (Teitelbaum & Friedman, 2008).

There are also numerous mariculture facilities where *T. squamosa* has been cultured successfully, but most are focused primarily on commercial production for the ornamental aquarium industry. We are aware of facilities in Fiji, Tonga, Cook Islands, Marshall Islands, Palau, Papua New Guinea, American Samoa, Samoa, FSM, Solomon Islands, Tuvalu, Vanuatu, Japan, Philippines, Malaysia, Indonesia, Thailand, Australia, and Hawaii (USA), which produce *T. squamosa* currently or did so in the past (Kittiwattanawong *et al.,* 2001; Lindsay *et al.,* 2004; Gomez & Mingoa-Licuanan, 2006; Teitelbaum & Friedman, 2008; Mies, Dor, *et al.,* 2017; Neo *et al.,* 2019). While many have experimented with outplanting cultured clams with the purpose of restocking natural populations, it seems that success of these efforts has been limited in most cases for reasons that have been discussed above (*e.g.,* difficulties in sustaining funding, monitoring, and protection). For example, the Marine Science Institute at the University of the Philippines produced 23,020 *T. squamosa* juveniles in October 2002 and distributed the clams throughout the

Mindanao region to restock natural populations (Gomez & Mingoa-Licuanan, 2006). The fate of this specific restocking effort has not been publicly reported, but other species that had been outplanted during the same period (primarily *T. gigas*) experienced high mortality in part due to a loss of institutional support, which limited the resources and personnel available to maintain and monitor the outplants (Gomez & Mingoa-Licuanan, 2006). Thus, it is likely that the *T. squamosa* suffered similarly low survivorship.

We are aware of two examples that have reported some measure of success in establishing sustainable populations of *T. derasa* in the wild. In Tonga, village-based nurseries of *T. squamosa* and *T. derasa* led to a notable increase in juvenile recruitment according to local accounts (Chesher, 1993). Villagers of Vava'u conveyed to the author that they had never seen so many young clams in surrounding reefs and that the children had collected and eaten ''baskets'' of them. This account, however, highlights the primary motivation of this effort, which was to replenish the natural giant clam stocks to support subsistence harvest, not to establish and conserve a sustainable population of the species. The most recent published survey of giant clams in the Vava'u area found that abundance of *T. squamosa* was very low, likely as a result of the ongoing harvest. Only 3 *T. derasa* and 10 *T. squamosa* were recorded in total across 27 survey sites in the area (Atherton *et al.,* 2014). Similarly, with significant financial support from the United States, FSM imported approximately 25,000 *T. derasa* from Palau in 1984–90 with the goal of establishing naturally reproducing populations on Yap and several of its outer atolls (Lindsay, 1995). Because the species is not endemic to FSM, researchers were able to easily monitor whether the introduced populations did indeed reproduce and recruit successfully. However, a number of challenges, including theft, neglect, limited aquaculture skills, and storm damage, led to large losses of introduced clams (Lindsay, 1995). At the time of the report in 1995, a small percentage (approximately 8 percent) of introduced *T. derasa* remained, but there was evidence of successful reproduction and recruitment of offspring on surrounding reefs. Surveys conducted by the Secretariat of the Pacific Community (PROC-Fish/C–CoFish programmes) noted the continued presence of *T. derasa* in Yap in low numbers in mid-2006 (Teitelbaum & Friedman, 2008).

We were not able to find any more recent monitoring data to indicate the current status of this introduced population, but with subsistence harvest of giant clams prevalent in FSM (Lindsay, 1995), it is unlikely to have grown significantly.

Beyond these examples, we could not find any other records documenting successful giant clam restocking initiatives. As is explained by Munro (1993b), efforts to replenish populations in areas where giant clams are still harvested should more accurately be viewed as ''a form of fishery enhancement,'' in that outplanted individuals will simply increase harvest volume rather than contribute to the conservation and long-term population growth of the species. In order to achieve significant conservation success, restocking initiatives must be accompanied by effective enforcement of harvest bans or an otherwise substantial reduction of harvest pressure on giant clams. However, as is discussed above, subsistence fishing for all giant clam species is ongoing throughout their respective ranges, and in most locations where harvest bans are in place, regulations are often poorly enforced.

There have also been a number of projects funded by the U.S. government seeking to explore markets, marketing strategies, and production economics for giant clams, with a particular focus on the Pacific islands that are subject to U.S. jurisdiction (Shang *et al.,* 1990, 1992; Leung *et al.,* 1994). As is described by Wells (1997), these projects have sponsored workshops on CITES and giant clam mariculture (Killelea-Almonte, 1992), funded hatchery development in American Samoa, and provided giant clam aquaculture training support for the U.S. Pacific Island territories. In American Samoa, *T. derasa, T. gigas,* and *H. hippopus* have all been cultured at the government hatchery with the ''main aim of establishing local farms to produce meat for local market'' (Wells, 1997). Wells (1997) reported that there were 6 lagoon nursery sites and 25 small-scale farms in operation in 1995, but the current status of each of these operations is not clear. According to Marra-Biggs et al. (2022), the ''stocks were harvested prior to reproduction and appear to be functionally extirpated.'' Samoa gifted approximately 650 *T. derasa* juveniles to American Samoa at the end of 2023, but similar to past giant clam nurseries, it appears that the primary ambition for this initiative is to establish a sustainable food source for the local community (American Samoa Department of Marine and Wildlife Resources Agency Report

2024). In Guam, a giant clam hatchery was established at the Guam Aquaculture Development and Training Center and in the past has received a number of shipments of *T. derasa* broodstock from the PMDC (Wells, 1997). However, many were lost due to damage from a cyclone in 1992, leaving approximately 100 specimens alive by 1994 (Wells, 1997). The current status of this initiative is not clear, but similar to American Samoa, many sources indicate that past attempts at giant clam mariculture in Guam have been plagued by persistent poaching. Heslinga *et al.* (1984) also noted that PMDC had shipped 500 *T. gigas* and 500 *T. squamosa* to the University of Guam Marine Laboratory ''to explore the possibility of reintroducing giant clams to areas where they are now extinct or very rare.'' However, we could not find any information indicating the outcome of these reintroductions, and later reports consistently consider *T. gigas* to be extinct in Guam (Munro, 1994; Pinca *et al.,* 2010; Neo *et al.,* 2017). Lastly, there is a report that *T. gigas* and *T. squamosa* were introduced to Keahole Point, Hawaii as part of a 5-year research project by Indo-Pacific Sea Farms to explore aquaculture of ornamental marine invertebrates for the aquarium trade (Heslinga, 1996). However, we are not aware of any efforts to outplant giant clams in Hawaii specifically for the purpose of establishing sustainable populations in the wild.

Thus, while there are many known mariculture facilities throughout the Indo-Pacific that have successfully bred and raised giant clams ex situ, there is little evidence that these initiatives further the protection or conservation of the seven species considered here. Without further information or survey data demonstrating such success, we consider the impact of these initiatives to be negligible with respect to the status of the species.

Proposed Listing Determinations

We have independently reviewed the best available scientific and commercial data, including the petition, public comments submitted in response to the 90-day finding (82 FR 28946, June 26, 2017), the Status Review Report, and other published and unpublished information. We considered each of the statutory factors to determine whether they contributed significantly to the extinction risk of each of the seven giant clam species considered here, alone or in combination with one another. As required by section 4(b)(1)(A) of the ESA, we also took into account efforts to protect the species by States, foreign

nations, or political subdivisions thereof, and evaluated whether those efforts provide a conservation benefit to the species.

Having considered this information in its entirety, we have determined that *H. porcellanus, T. mbalavuana,* and *T. squamosina* are presently in danger of extinction throughout the entirety of their respective ranges, *T. derasa* and *T. gigas* are in danger of extinction in a significant portion of their respective ranges, and *H. hippopus* is likely to become an endangered species within the foreseeable future in a significant portion of its range. Therefore, we propose to list *H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina* as endangered species and *H. hippopus* as a threatened species under the ESA. We have determined that the fluted clam (*T. squamosa*) is not currently in danger of extinction throughout all or a significant portion of its range and is not likely to become so within the foreseeable future. Therefore, we find that *T. squamosa* does not meet the definition of a threatened or an endangered species under section $4(a)(1)$ of the ESA.

This finding is consistent with the statute's requirement to base our findings on the best scientific and commercial data available, which is summarized and analyzed above, and discussed in more detail in Rippe *et al.* (2023).

Similarity of Appearance

As discussed in the section titled *Overutilization for Commercial, Recreational, Scientific, or Educational Purposes,* giant clams and their derivative products (*e.g.,* meat, shells, and shell carvings) are traded extensively in international markets and are commonly imported into the United States. Beginning in 2009, U.S. customs officials began encountering regular shipments of giant clam meat from Pacific island nations, chiefly from the Marshall Islands and FSM, but also from Fiji, Tonga, Palau, Samoa, Kiribati, and French Polynesia. Law enforcement personnel report that the meat is typically frozen in plastic bags or bottles and is often shipped in coolers mixed together with various other seafood products. The shipments are very rarely accompanied by valid CITES permits and are therefore nearly always seized or refused entry at the border when discovered.

LEMIS trade data provided by USFWS indicate that an average of 127 shipments of giant clam meat originating from the Marshall Islands and FSM were seized or refused entry at U.S. ports of entry per year from 2016

to 2020. These shipments equated to approximately 233 kg and 4,504 specimens per year, reflecting shipments recorded by weight and by number of specimens, respectively. Furthermore, over the past two years, U.S. law enforcement has documented an additional 250 cases of giant clam meat violations and seizures between December 2021 and October 2023 (S. Valentin, USFWS Office of Law Enforcement, pers. comm., November 8, 2023). The LEMIS trade data also reveal an average of 9 shipments of shell carvings, jewelry, and other worked shell products into the United States per year from 2016 to 2020. These shipments comprise approximately 152 specimens per year on average, in most cases without record of the location or species of origin.

Critically, for derivative giant clam parts and products, such as meat that has been removed from the shell and worked shell items (*i.e.,* carvings and jewelry), law enforcement personnel are not able to visually determine or verify the species from which the product is derived. Therefore, it is possible that these shipments may have contained any of the six giant clam species that are proposed for listing based on their extinction risk (*i.e., H. hippopus, H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina*).

Section 4(e) of the ESA authorizes the treatment of a species, subspecies, or population segment as endangered or threatened if: ''(a) such species so closely resembles in appearance, at the point in question, a species which has been listed pursuant to such section that enforcement personnel would have substantial difficulty in attempting to differentiate between the listed and unlisted species; (b) the effect of this substantial difficulty is an additional threat to an endangered or threatened species; and (c) such treatment of an unlisted species will substantially facilitate the enforcement and further the policy of this Act.''

The aforementioned reports from U.S. law enforcement personnel make it clear that the similarity of appearance between worked products derived from the species that are proposed for listing (*i.e., H. hippopus, H. porcellanus, T. derasa, T. gigas, T. mbalavuana, T. squamosina*) and those from the species that are not proposed for listing (*i.e., T. crocea, T. maxima, T. noae,* and *T. squamosa*) causes substantial difficulty for law enforcement personnel in attempting to differentiate between the six species proposed for listing and the other four species that are not. Law enforcement personnel have expressed confidence in distinguishing the meat of

giant clams from that of other marine fauna based on visual characteristics, but note that visual differentiation between giant clam species is not possible.

Furthermore, the difficulty in distinguishing the species from which worked products are derived is an additional threat to the six species proposed to be listed under section 4(a)(1) of the Act. Due to the inadequacy of existing regulations, lack of enforcement capacity, and typical harvesting practices in most Pacific island nations (see sections titled *Overutilization for Commercial, Recreational, Scientific, or Educational Purposes* and *The Inadequacy of Existing Regulatory Mechanisms*), it is possible, if not likely, that giant clam specimens reaching U.S. ports are harvested opportunistically with little regard for the species collected. Moreover, neither the Marshall Islands nor FSM are signatories to CITES and have not demonstrated the capacity to assess and regulate the trade of protected species. Because of these regulatory inadequacies and the aforementioned U.S. enforcement challenges, it is feasible that persons engaging in commerce involving derivative products from one of the six species proposed to be listed could misrepresent, either accidentally or purposefully, that such products are derived from a species that has not been proposed for listing. For example, a recent forensic investigation revealed that several recent seizures of giant clam meat contained specimens that were identified genetically as *H. hippopus, T. gigas,* and *T. maxima,* a combination of species that are and are not proposed to be listed. The meat of the three species was otherwise indistinguishable by law enforcement personnel, highlighting the substantial difficulty in differentiating the species visually and the potential for those species that are proposed to be listed as threatened or endangered to be misrepresented as species that are not proposed to be listed in shipments to the United States. In addition, given the significant volume of giant clam meat and shell products intercepted by law enforcement personnel on a regular basis, it is not always possible to conduct detailed forensic analyses due to a limited capacity to store and process the samples on site.

In order for the ESA's import and export restrictions to be effective, enforcement personnel must be able to quickly determine whether derivative parts or products are from a listed species at U.S. ports of entry and take appropriate enforcement action to suppress illegal trade. Misrepresentation

of the species of giant clam would prevent effective enforcement of the import and export restrictions on the species proposed to be listed, because enforcement personnel will not be able to visually determine which species derivative parts or products are from. The high risk of misrepresentation, coupled with the visual similarity of certain derivative part or products of giant clams species, creates a loophole that would undermine the effectiveness of import and export restrictions imposed under section 9(a)(1)(A) of the ESA. The effect of this loophole—the weakened deterrent value of the Act in protecting the species proposed to be listed due to the substantial difficulty in visually distinguishing derivative parts or products among different species of giant clams—is an additional threat to the species that we propose to list under section $4(a)(1)$.

The similarity of appearance regulation proposed by NMFS in this action would substantially facilitate enforcement of the ESA's import and export restrictions, because it would allow enforcement personnel to easily identify and take enforcement action when they identify derivative parts or product from giant clams at U.S. ports of entry. Without a similarity of appearance regulation, derivative parts and products from a listed giant clam species could easily be mislabeled and imported to or exported from the U.S. This would substantially undermine the enforcement of regulations under section 9(a)(1) and section 4(d) for the protection of the proposed endangered and threatened species, respectively. We therefore propose to list *T. crocea, T. maxima, T. noae,* and *T. squamosa* as threatened species under the authority of section 4(e) of the ESA. These four species have ranges that overlap the Pacific region where virtually all of the shipments of giant clam meat to the U.S. originate. Taking this action would alleviate an enforcement challenge that has the potential to contribute to unauthorized commerce of endangered and threatened giant clam species in the U.S. and would provide for the conservation of these species under the ESA.

Effects of This Rulemaking

Conservation measures provided for species listed as endangered or threatened under the ESA include recovery actions (16 U.S.C. 1533(f)); concurrent designation of critical habitat, if prudent and determinable (16 U.S.C. 1533(a)(3)(A)); Federal agency requirements to consult with NMFS under section 7 of the ESA to ensure their actions are not likely to jeopardize

the species or result in adverse modification or destruction of critical habitat should it be designated (16 U.S.C. 1536); and, for endangered species, prohibitions on ''taking'' (16 U.S.C. 1538). Recognition of the species' plight through listing also promotes conservation actions by Federal and State agencies, foreign entities, private groups, and individuals.

Identification of Those Activities That Would Constitute a Violation of Section 9 of the ESA

All of the prohibitions of section 9(a)(1) of the ESA will apply to the five species of giant clams that are proposed to be listed as endangered (*i.e., H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina*), should the proposed rule be adopted. We are also proposing to extend the section 9(a)(1) prohibitions to *H. hippopus.* Section 9(a)(1) prohibits import; export; delivery, receipt, carriage, transport, or shipment in interstate or foreign commerce of the species, by any means whatsoever and in the course of commercial activity; or sale or offer for sale in interstate or foreign commerce. Section 9(a)(1) also prohibits take within the United States or on the high seas; or to possess, sell, deliver, carry, transport, or ship a species that has been taken in violation of the ESA.

On July 1, 1994, NMFS and USFWS published a policy (59 FR 34272) that requires us to identify, to the maximum extent practicable at the time a species is listed, those activities that would or would not constitute a violation of section 9 of the ESA. The intent of this policy is to increase public awareness of the effect of a listing on proposed and ongoing activities within a species' range. Based on available information, we believe that the following categories of activities are most likely to result in a violation of the ESA section 9 prohibitions should the proposed rule be adopted. We emphasize that whether a violation results from a particular activity is dependent on the facts and circumstances of each incident. The mere fact that an activity may fall within one of the categories does not mean that the specific activity will cause a violation; due to such factors as location and scope, specific actions may not result in direct or indirect adverse effects on a species. Further, an activity not listed may in fact result in a violation. However, based on currently available information, we believe the following types of activities that could result in a violation of section 9 prohibitions include, but are not limited to, the following:

(1) Take of any listed species within the U.S. or its territorial sea, or upon the high seas. Take is defined in section 3 of the ESA as ''to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct'';

(2) Possessing, delivering, transporting, or shipping any individual or part of listed species (dead or alive) taken in violation of section 9(a)(1)(B) or $9(a)(1)(C)$;

(3) Delivering, receiving, carrying, transporting, or shipping in interstate or foreign commerce any individual or part of listed species, in the course of a commercial activity, even if the original taking was legal;

(4) Selling or offering for sale in interstate or foreign commerce any part of listed species, except antique articles at least 100 years old;

(5) Exporting or importing any individual or part of listed species to or from any country;

(6) Releasing captive or cultured specimens of listed species into the wild. Although specimens held noncommercially in captivity at the time of listing are exempt from certain prohibitions, the individual animals are considered listed and afforded most of the protections of the ESA, including most importantly the prohibitions against injuring or killing of endangered species. Release of a captive animal has the potential to injure or kill the animal. Of an even greater conservation concern, the release of a captive animal has the potential to affect wild populations through introduction of diseases or inappropriate genetic mixing. Depending on the circumstances of the case, NMFS may authorize the release of a captive animal through a section $10(a)(1)(A)$ permit;

(7) Altering the habitat of listed species in such a way that results in injury or death of the species, such as removing or altering substrate or other physical structures, activities resulting in elevated water temperatures that lead to bleaching or other degradation of the physiological functions of listed species, and activities resulting in altered water chemistry and/or water acidification that lead to reduced calcification rates, reproductive impairment, or other degradation of physiological functions of listed species; and

(8) Discharging pollutants or organic nutrient-laden water, including sewage water, into the habitat of listed species to an extent that harms or kills listed species.

This list provides examples of the types of activities that are likely to cause a violation, but it is not exhaustive. Persons or entities concluding that their

activity is likely to violate the ESA are encouraged to immediately adjust that activity to avoid violations and to seek authorization under: (a) an ESA section 10(a)(1)(B) incidental take permit; (b) an ESA section $10(a)(1)(A)$ research and enhancement permit; or (c) an ESA section 7 consultation. The public is encouraged to contact us (see **FOR FURTHER INFORMATION CONTACT**) for assistance in determining whether circumstances at a particular location, involving these activities or any others, might constitute a violation of the ESA. Furthermore, the scientific research community is encouraged to submit applications for research to be conducted on *H. hippopus, H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina* so that the research can continue uninterrupted should this proposed rule be adopted.

Identification of Those Activities That Would Not Constitute a Violation of Section 9 of the ESA

We have also identified, based on information available at this time, categories of activities that are not considered likely to result in a violation of section 9 should the proposed rule be adopted. As noted above, whether a violation results from a particular activity is entirely dependent on the facts and circumstances of each incident, and it is possible that specific actions taken on this list may in fact result in a violation. However, although not binding, we consider the following actions as not likely to result in violations of ESA section 9:

(1) Take authorized by, and carried out in accordance with the terms and conditions of, an ESA section 10(a)(1)(A) permit issued by NMFS for purposes of scientific research or the enhancement of the propagation or survival of the listed species;

(2) Incidental take of a listed species resulting from Federally authorized, funded, or conducted projects for which consultation under section 7 of the ESA has been completed, and when the otherwise lawful activity is conducted in accordance with any terms and conditions granted by NMFS in an incidental take statement of a biological opinion pursuant to section 7 of the ESA;

(3) Continued possession of listed species that were in captivity at the time of listing, including any progeny produced from captive specimens after the rule is finalized, so long as the prohibitions of ESA section 9(a)(1) are not violated. Specimens are considered to be in captivity if they are maintained in a controlled environment (*e.g.,* landbased aquaria) or under human care in

open-water nurseries (*i.e.,* protected nearshore enclosures under the active management of humans). Specimens are not considered to be in captivity if they have been outplanted to a natural habitat or restoration site. Individuals or organizations should be able to provide evidence that specimens or parts of listed species were in captivity prior to their listing. Captive specimens may be non-commercially exported or imported; however, the importer or exporter must be able to provide evidence to show that the parts meet the criteria of ESA section 9(b)(1) (*i.e.,* held in a controlled environment at the time of listing, in a non-commercial activity);

(4) Providing normal care for legallyobtained captive specimens of listed species. Normal care includes handling, cleaning, maintaining water quality within an acceptable range, extracting tissue samples for the purposes of disease diagnosis or genetics, and treating of maladies such as disease or parasites using established methods proven to be effective;

(5) Interstate transportation of legallyobtained captive specimens or parts of listed species, provided it is not in the course of a commercial activity. If captive specimens of listed species are to be moved to a different holding location, records documenting the transfer should be maintained;

(6) Use of captive specimens of listed species for scientific studies under the authorization of an ESA section 10(a)(1)(A) permit issued by NMFS;

(7) Import or export of live specimens or parts of listed species with all accompanying CITES export permits and an ESA section 10(a)(1)(A) permit for purposes of scientific research or the enhancement of the propagation or survival of the species.

Protective Regulations for Threatened Species Under Section 4(d) of the ESA

We are proposing to list *H. hippopus* as a threatened species under section 4(a)(1). The ESA does not specify particular prohibitions for threatened species. For species listed as threatened, the second sentence in section 4(d) of the ESA authorizes the Secretary to extend any or all of the prohibitions identified in section $9(a)(1)$ for endangered species to threatened species. We therefore propose to extend the section 9(a)(1) prohibitions in protective regulations issued under the second sentence of section 4(d) to *H. hippopus.* No special findings are required to support extending section 9 prohibitions for the protection of threatened species. *See In re Polar Bear Endangered Species Act Listing and 4(d) Rule Litigation,* 818 F.Supp.2d 214, 228

(D.D.C. 2011); *Sweet Home Chapter of Cmties. for a Great Oregon* v. *Babbitt,* 1 F.3d 1, 8 (D.C. Cir. 1993), *modified on other grounds on reh'g,* 17 F.3d 1463 (D.C. Cir. 1994), *rev'd on other grounds,* 515 U.S. 687 (1995).

We are also proposing to list *T. crocea, T. maxima, T. noae,* and *T. squamosa* as threatened species under section 4(e) of the ESA. Because these listings are being proposed on the basis of similarity of appearance rather than the extinction risk of these four species, we are not proposing to extend the section 9(a)(1) prohibitions to these species in a blanket fashion. Rather, we aim to facilitate the protection of *H. hippopus, H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina* by mitigating the challenge that law enforcement personnel face in determining the species of origin for derivative parts and products of giant clams, such as meat and shell carvings, in imports and exports into and from the United States and its territories.

To do so, we are proposing to apply the ESA section $9(a)(1)(A)$ prohibition of import into and export from the United States and its territories to *T. crocea, T. maxima, T. noae,* and *T. squamosa,* but limit the prohibition to derivative parts and products for which the species of origin cannot be visually determined. For the purpose of this regulation, ''derivative parts and products'' are defined as: (a) any tissue part that has been removed from the shell, including mantle tissue, adductor muscle, portions thereof, or the whole flesh of the animal comprising both the mantle and adductor muscle; (b) any worked shell product, including handicrafts, sculptures, jewelry, tableware, decorative ornaments, and other carvings, but not raw, unworked shells; and (c) pearls or any product derived from a pearl. This prohibition would apply to commercial and noncommercial shipments of any such products of *T. crocea, T. maxima, T. noae,* and *T. squamosa* and would make it unlawful for any person subject to the jurisdiction of the United States to import such products into or export such products from the United States or its territories.

No other prohibitions under section 9 of the ESA are proposed to be extended to these four species. A person would continue to be able to possess, deliver, carry, transport, ship, sell, or offer to sell *T. crocea, T. maxima, T. noae,* and *T. squamosa,* and their parts and products, domestically and in interstate and foreign commerce. We have information indicating that all four of these species occur within the waters of at least one U.S. Pacific Island territory.

T. maxima, in particular, is the target of several mariculture initiatives intended to establish a sustainable source of food and income for communities in American Samoa, Guam, and CNMI. The best available scientific and commercial information indicates that none of the other six species that we are proposing to list as endangered or threatened based on their extinction risk are still extant within U.S. waters. Therefore, it is unlikely that domestic activities and interstate commerce involving *T. crocea, T. maxima, T. noae,* or *T. squamosa* would threaten the status or recovery of *H. hippopus, H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina* throughout their current range. For this reason, we are not proposing to prohibit these activities.

We are also not proposing to prohibit the import or export of live or intact specimens or raw, unworked shells of *T. crocea, T. maxima, T. noae, T. squamosa* into or from the United States and its territories. As mentioned above, there are several initiatives within the United States focused on culturing one or more of *T. crocea, T. maxima, T. noae,* and *T. squamosa* for the purpose of providing food and income to local communities. These operations often rely on the international trade of live broodstock or juveniles between mariculture facilities to initiate or supplement a culture stock. We have no information to suggest that live or intact specimens or raw, unworked shells of giant clams are being misrepresented as incorrect species in imports or exports into or from the United States, nor that law enforcement personnel have substantial difficulties visually differentiating the species of origin for such shipments. Thus, there is little risk that imports or exports of live or intact *T. crocea, T. maxima, T. noae,* and *T. squamosa* or raw, unworked shells of these species into or from the United States or its territories would threaten the status or recovery of *H. hippopus, H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina* in the wild. We are therefore not proposing to prohibit those activities.

Identifying Section 7 Conference and Consultation Requirements

Section 7(a)(4) (16 U.S.C. 1536(a)(4)) of the ESA and NMFS/USFWS regulations (50 CFR 402.10) require Federal agencies to confer with NMFS on actions likely to jeopardize the continued existence of species proposed for listing, or that are likely to result in the destruction or adverse modification of proposed critical habitat of those species. If a proposed species is

ultimately listed, under section 7(a)(2) (16 U.S.C. 1536(a)(2)) of the ESA and the NMFS/USFWS regulations (50 CFR part 402), Federal agencies must consult on any action they authorize, fund, or carry out if those actions may affect the listed species or its critical habitat to ensure that such actions are not likely to jeopardize the continued existence of the species or result in adverse modification or destruction of critical habitat should it be designated. Examples of Federal actions that may affect giant clams include, but are not limited to: alternative energy projects, discharge of pollution from point sources, non-point source pollution, contaminated waste disposal, dredging, pile-driving, development of water quality standards, and military activities.

Critical Habitat

Critical habitat is defined in section 3 of the ESA (16 U.S.C. 1532(3)) as: (1) the specific areas within the geographical area occupied by a species, at the time it is listed in accordance with the ESA, on which are found those physical or biological features (a) essential to the conservation of the species and (b) that may require special management considerations or protection; and (2) specific areas outside the geographical area occupied by a species at the time it is listed upon a determination that such areas are essential for the conservation of the species. ''Conservation'' means the use of all methods and procedures needed to bring the species to the point at which listing under the ESA is no longer necessary. Section 4(a)(3)(A) of the ESA $(16 \text{ U.S.}\text{C. } 1533(a)(3)(A))$ requires that, to the extent prudent and determinable, critical habitat be designated concurrently with the listing of a species. Designations of critical habitat must be based on the best scientific data available and must take into consideration the economic, national security, and other relevant impacts of specifying any particular area as critical habitat. Critical habitat cannot be designated within foreign countries or in other areas outside the jurisdiction of the United States (50 CFR 424.12(g)). Thus, with respect to *H. porcellanus, T. mbalavuana,* and *T. squamosina,* which have highly restricted ranges that are entirely outside the jurisdiction of the United States, we cannot designate any areas as critical habitat within their occupied ranges.

At this time, critical habitat is not yet determinable for *H. hippopus, T. derasa,* and *T. gigas,* which are believed to occur in areas under U.S. jurisdiction, because data sufficient to perform

required analyses are lacking. *See* 50 CFR 424.12(a)(2). Therefore, we are not proposing to designate critical habitat for these species at this time. However, we invite public comments on physical and biological features and areas in U.S. waters that may be essential to these species and well as any other information that may inform our consideration of designating critical habitat for these three species (see Public Comments Solicited).

Designation of critical habitat would not be applicable to *T. crocea, T. maxima, T. noae,* and *T. squamosa,* because these species are proposed to be listed due to their similarity of appearance to *H. hippopus, H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina,* rather than on the basis of their extinction risk.

Role of Peer Review

In December 2004, the Office of Management and Budget (OMB) issued a Final Information Quality Bulletin for Peer Review establishing minimum peer review standards, a transparent process for public disclosure of peer review planning, and opportunities for public participation. The OMB Bulletin, implemented under the Information Quality Act (Pub. L. 106–554) is intended to enhance the quality and credibility of the Federal Government's scientific information, and applies to influential or highly influential scientific information disseminated on or after June 16, 2005. To satisfy our requirements under the OMB Bulletin, we obtained independent peer review of the draft Status Review Report. Three independent specialists were selected from the academic and scientific community for this review. After substantial revision of the Status Review Report following an initial round of peer review, one of the reviewers agreed to provide a second review of the updated version, and one additional review was received from a fourth expert from the scientific community. All peer reviewer comments were addressed prior to dissemination of the Status Review Report and publication of this document. The peer review report can be found online (see **ADDRESSES**).

Public Comments Solicited

To ensure that the final action resulting from this proposal will be as accurate and effective as possible, we solicit comments and suggestions from the public, other governmental agencies, the scientific community, industry, environmental groups, territorial governments, cultural practitioners, indigenous communities, and any other interested parties. Comments are

encouraged on this proposal (see **DATES** and **ADDRESSES**). Specifically, we are interested in information regarding: (1) new or updated information regarding the range, distribution, and abundance of the six giant clam species proposed for listing based on their extinction risk (*H. hippopus, H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina*); (2) new or updated information regarding their genetics and population structure; (3) habitat within their range that was present in the past but may have been lost over time; (4) new or updated biological or other relevant data concerning any threats to these giant clams; (5) current or planned activities within their range and the possible impact of these activities on the relevant species; (6) recent observations or sampling of *H. hippopus, H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina*; and (7) efforts being made to protect or recover natural populations of these species, and documented results of such efforts.

Public Comments Solicited on Critical Habitat

We request information describing the quality and extent of habitats for the three giant clam species proposed for listing based on their extinction risk and that occur in areas under U.S. jurisdiction (*i.e., H. hippopus, T. derasa,* and *T. gigas*), as well as information on areas that may qualify as critical habitat for these three species in U.S. waters. Specific areas that include the physical and biological features essential to the conservation of the species, where such features may require special management considerations or protection, should be identified. Areas outside the occupied geographical area should also be identified, if such areas may be essential to the conservation of the species. As noted previously, ESA implementing regulations at 50 CFR 424.12(g) specify that critical habitat shall not be designated within foreign countries or in other areas outside of U.S. jurisdiction. Therefore, we request information only on potential areas of critical habitat within waters under U.S. jurisdiction.

Section 4(b)(2) of the ESA requires the Secretary to consider the economic impact, impact on national security, and any other relevant impact of designating a particular area as critical habitat. Section 4(b)(2) also authorizes the Secretary to exclude from a critical habitat designation those particular areas where the Secretary finds that the benefits of exclusion outweigh the benefits of designation, unless excluding that area will result in

extinction of the species. For features and areas potentially qualifying as critical habitat, we also request information describing: (1) Activities or other threats to the essential features or activities that could be affected by designating them as critical habitat; and (2) the positive and negative economic, national security and other relevant impacts, including benefits to the recovery of the species, likely to result if these areas are designated as critical habitat. We seek information regarding the conservation benefits of designating areas within waters under U.S. jurisdiction as critical habitat. In keeping with the guidance provided by OMB (2000; 2003), we seek information that would allow the monetization of these effects to the extent possible, as well as information on qualitative impacts to economic values.

Data reviewed may include, but are not limited to: (1) scientific or commercial publications; (2) administrative reports, maps or other graphic materials; (3) information received from experts; and (4) comments from interested parties. Comments and data particularly are sought concerning: (1) maps and specific information describing the abundance and distribution of *H. hippopus, T. derasa,* and/or *T. gigas,* as well as any additional information on occupied and unoccupied habitat areas; (2) the reasons why any habitat should or should not be determined to be critical habitat as provided by sections 3(5)(A) and 4(b)(2) of the ESA; (3) information regarding the benefits of designating particular areas as critical habitat; (4) current or planned activities in the areas that might be proposed for designation and their possible impacts; and (5) any foreseeable economic or other potential impacts resulting from designation, and in particular, any impacts on small entities.

You may submit your comments and supporting information concerning this proposal electronically, by mail (see **ADDRESSES**), or during public hearings (see **DATES**). The proposed rule and supporting documentation can be found on the Federal eRulemaking Portal at *<https://www.regulations.gov>* by entering *NOAA–NMFS–2017–0029* in the Search box.

Public Informational Meetings and Public Hearings

Section 4(b)(5)(E) of the ESA requires us to promptly hold at least one public hearing if any person requests one within 45 days of publication of a proposed rule to implement a species listing determination. Public hearings provide a forum for accepting formal

verbal comments on this proposed rule. Prior to each public hearing, we will provide an overview of the proposed rule during a public informational meeting. In-person and virtual public hearings on this proposed rule will be held during the public comment period at dates, times, and locations to be announced in a forthcoming **Federal Register** notice. Requests for additional public hearings must be made in writing (see **ADDRESSES**) by September 9, 2024.

References

A complete list of the references used in this proposed rule is available upon request (see **FOR FURTHER INFORMATION CONTACT**).

Classification

National Environmental Policy Act (NEPA)

The 1982 amendments to the ESA, in section $4(b)(1)(A)$, restrict the information that may be considered when assessing species for listing. Based on this limitation of criteria for a listing decision and the opinion in *Pacific Legal Foundation* v. *Andrus,* 675 F. 2d 825 (6th Cir. 1981), we have concluded that ESA listing actions are not subject to the environmental assessment requirements of NEPA (see NOAA Administrative Order 216–6A (2016) and the companion manual, ''Policy and Procedures for Compliance with the National Environmental Policy Act and Related Authorities,'' which became effective January 13, 2017 (''Companion Manual''), at 2).

Further, we conclude that extension of the ESA section 9(a)(1) protections in a blanket or categorical fashion is a form of ministerial action taken under the authority of the second sentence of ESA section 4(d). Courts have found that it is reasonable to interpret the second sentence of section 4(d) as setting out distinct authority from that of the first sentence, which is invoked when the agency proposes tailored or special protections that go beyond the standard section 9 protections. See *In re Polar Bear Endangered Species Act Listing and 4(d) Rule Litigation,* 818 F. Supp. 2d 214, 228 (D.D.C. 2011); *Sweet Home Chapter of Cmties. for a Great Oregon* v. *Babbitt,* 1 F.3d 1, 8 (D.C. Cir. 1993), *modified on other grounds on reh'g,* 17 F.3d 1463 (D.C. Cir. 1994), *rev'd on other grounds,* 515 U.S. 687 (1995). This type of action is covered under the NOAA categorical exclusion G7, which applies to ''policy directives, regulations and guidelines of an administrative, financial, legal, technical or procedural nature . . .'' See Companion Manual, Appx. E. None of the extraordinary

circumstances identified in § 4.A. of the Companion Manual apply.

However, the promulgation of ESA section 4(d) protective regulations in association with the proposed listing of *T. crocea, T. maxima, T. noae,* and *T. squamosa* as threatened species is subject to the requirements of NEPA and we have prepared a draft Environmental Assessment (EA) analyzing the proposed 4(d) regulation for these species and alternatives. We are seeking comment on the draft EA, which is available on the Federal eRulemaking Portal (*<https://www.regulations.gov/>*) or upon request (see **DATES** and **ADDRESSES**, above).

Regulatory Flexibility Act

As noted in the Conference Report on the 1982 amendments to the ESA, economic impacts cannot be considered when assessing the status of a species. Therefore, the economic analyses required by the Regulatory Flexibility Act are not applicable to the listing process nor the ministerial extension of the section 9(a) prohibitions to *H. hippopus*.

However, the promulgation of ESA section 4(d) protective regulations in association with the proposed listing of *T. crocea, T. maxima, T. noae,* and *T. squamosa* as threatened species is subject to the requirements of the Regulatory Flexibility Act. We have prepared an initial regulatory impact analysis (IRFA) in accordance with section 603 of the Regulatory Flexibility Act (5 U.S.C. 601, *et seq.*). The IRFA analyzes the impacts to small entities that may be affected by the proposed 4(d) regulations for *T. crocea, T. maxima, T. noae,* and *T. squamosa.* To review the IRFA, see the **ADDRESSES** section above. We welcome comments on this IRFA, which is summarized below.

The IRFA first identified the types and approximate number of small entities that would be subject to regulation under the proposed rule. It then evaluated the potential for the proposed rule to incrementally impact small entities (*i.e.,* result in impacts to small entities beyond those that would be incurred due to existing regulations but absent the proposed rule). The IRFA was informed by data gathered from the Small Business Administration (SBA), Dun and Bradstreet, Inc., the CITES trade database, and the LEMIS trade database.

The IRFA examined the potential economic impacts on small entities of the proposed prohibition on the import and export of derivative parts and products of *T. crocea, T. maxima, T. noae,* and *T. squamosa* into and from

the United States. It focused specifically on products that would otherwise be cleared by U.S. Customs and Border Protection officials and whose purpose of import or export is either commercial trade or non-personal exhibition. The prohibition on import or export of products coded as personal property by U.S. Customs and Border Protection officials would not impact a small business or other small entity, and any imports or exports of parts accompanied by both a valid CITES export permit and an ESA section 10(a)(1)(A) permit for purposes of scientific research or the enhancement of the propagation or survival of the species would be exempted from the proposed prohibition.

The IRFA anticipates that the proposed prohibition on the import and export of derivative parts and products of *T. crocea, T. maxima, T. noae,* and *T. squamosa* would apply to thousands of small entities, but that only a small subset of these small entities would be impacted and impacts would be minor. Any additional costs associated with enforcement of the rule would be incurred by government agencies that do not qualify as small entities, and it is unlikely that the proposed rule would affect any small governmental jurisdictions.

The small entities most likely to be directly impacted by the proposed rule include those classified under the North American Industry Classification System (NAICS) as Jewelry, Watch, Precious Stone, and Precious Metal Merchant Wholesalers (NAICS industry code 423940) and Museums (NAICS industry code 712110). According to data gathered from the Dun and Bradstreet Hoovers database, there are approximately 25,000 U.S. small entities classified as Jewelry, Watch, Precious Stone, and Precious Metal Merchant Wholesalers and approximately 47,000 museums in the U.S. that qualify as small entities. Under the proposed rule, wholesalers could lose revenue that would otherwise be generated through the importation and sale, or exportation, of the derivative parts and products for commercial purposes. Museums or similar entities that would otherwise import and exhibit derivative parts and products could lose revenue if attendance declines as a result of an artistic item not being exhibited.

LEMIS trade data provided by the USFWS for the years 2016–2020 indicate that there were two imports into and two exports from the 50 states and the District of Columbia over these years of derivative parts or products of giant clams that were cleared by U.S. Customs and Border Protection officials and whose purpose of import or export was either commercial trade or nonpersonal exhibition. As there is no basis for expecting an increase in the rate of U.S. import or export of derivative parts or products of giant clams over the foreseeable future, the IRFA assumes that the number, type, and dollar value of imports and exports of these products over the years 2016–2020 reasonably represents the composition of trade of these products that would occur in the future, absent the proposed rule. Based on a combined value of \$19,000 of U.S. imports and exports of derivative parts or products of giant clams from 2016 to 2020 for the purpose of commercial trade, this IRFA estimates that the proposed rule would result in annualized impacts on wholesalers of \$3,700 (2023 dollars). Revenue losses to museums cannot be quantified with available data but are expected to be minor, as there was only one import into and one export from the U.S. of a derivative product of giant clams between the years 2016–2020 for the purpose of exhibition in a museum. The item, a carving valued at \$44,000 (2023 dollars), was imported into and then exported from the U.S. in 2018. While it is possible that the proposed rule could result in a small entity wholesaler or museum with low annual revenue bearing impacts that constitute a large percentage of their annual revenue, this outcome is highly uncertain. Based on the low volume of annual U.S. imports and exports of derivative parts or products of giant clams, it is more likely that impacts on small entities would be minor and limited to a very small number of small entities.

The RFA requires consideration of any significant alternatives to the proposed rule that would accomplish the stated objectives of the applicable statutes and would minimize significant economic impacts to small entities. We considered the following alternatives when developing this proposed rule.

Alternative 1. No-action Alternative. Under the No-action Alternative, NMFS would not apply any protective regulations in association with the proposed listing of *T. crocea, T. maxima, T. noae,* and *T. squamosa* as threatened species under section 4(e) of the ESA, and there would be no change from current management policies of these four species. Alternative 1 represents the regulatory status quo with respect to *T. crocea, T. maxima, T. noae,* and *T. squamosa,* but assumes that *H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina* would be listed as endangered and *H. hippopus* would be listed as threatened

under the ESA due to their extinction risk.

Without a prohibition on the import into and export from the U.S. of derivative parts and products derived from *T. crocea, T. maxima, T. noae,* and *T. squamosa,* derivative parts and products derived from any of the six species proposed to be listed due to their extinction risk could be misidentified by law enforcement officials as deriving from these four species. Thus, Alternative 1 would undermine the listing of *T. crocea, T. maxima, T. noae,* and *T. squamosa* based on the similarity of appearance of their derivative products to those of the six species proposed to be listed due to their extinction risk, as their listing would provide no incremental benefit to the survival and recovery of six species proposed to be listed as endangered or threatened. No incremental impacts would be borne by small (or large) entities, but *H. hippopus, H. porcellanus, T. derasa, T. gigas, T. mbalavuana,* and *T. squamosina* would continue to be at risk of further declines in abundance and increased risk of extinction due to international trade of their derivative parts and products. Thus, Alternative 1 is not a reasonable alternative.

Alternative 2. Proposed Alternative. Under the Proposed Alternative, the import into and export from the U.S. of derivative parts and products from *T. crocea, T. maxima, T. noae,* and *T. squamosa* would be prohibited. This alternative would allow for import into and export from the U.S. of live and intact specimens and raw, unworked shells of these species, as well as the delivery, receipt, carry, transport, or shipment, and sale or offer for sale of these species and their derivative parts and products in interstate commerce. Impacts on small entities would be limited to revenue losses borne by small entity wholesalers or museums or other non-personal exhibitors of giant clam products that, absent the Proposed Alternative, would engage in the import and/or export of parts and products derived from these four species. Small entities that, absent the Proposed Alternative, would engage in the export of parts and products derived from maricultured *T. crocea, T. maxima, T. noae,* and *T. squamosa* specimens would be impacted to the extent that they would otherwise generate revenue from such exports. However, no information is available suggesting this type of international trade would occur over the foreseeable future in the absence of the Proposed Action. Alternative 2 was selected as the Proposed Alternative because it would

contribute to the survival and recovery of six species of giant clams proposed to be listed as endangered or threatened due to their extinction risk without constraining international trade of live or intact specimens or shells of *T. crocea, T. maxima, T. noae,* and *T. squamosa,* or domestic activities involving these four species.

Alternative 3. Application of All ESA section 9(a)(1) Prohibitions (Full Action Alternative). Alternative 3 would apply all section 9(a)(1) prohibitions of the ESA to *T. crocea, T. maxima, T. noae,* and *T. squamosa.* Prohibitions under this alternative would include, but not be limited to, the import, export, possession, sale, delivery, carrying, transport, or shipping of these species including live or intact specimens and shells—in interstate or foreign commerce or for commercial activity. Imports and exports of live specimens would be permitted under the Proposed Alternative but prohibited under Alternative 3, which, relative to the Proposed Action and No-action Alternative, would incrementally impact small entities to the extent that they would otherwise generate revenue from sale of these four species of giant clams or their derivative products. The total value of U.S. imports of live specimens of *T. crocea, T. maxima, T. noae,* and *T. squamosa* from 2016 to 2020 was approximately \$3.12 million (2023 dollars), while exports had a total value of approximately \$113,000. Small businesses in the Pet and Supplies Retailers and Other Miscellaneous Nondurable Goods Merchant Wholesalers industries (NAICS codes 424990 and 459910) would bear the vast majority of these impacts, which would likely be concentrated among a small number of companies. Incremental impacts of Alternative 3 on small entities could also be substantially greater than those that would occur under the Proposed Alternative in part because the prohibitions on take and interstate commerce would significantly constrain the development of giant clam mariculture projects in the U.S., notably those in the U.S. Pacific Island territories. Alternative 3 would impact small entities to the extent that they would otherwise generate revenue from these mariculture projects. Alternative 3 would likely result in substantially greater impacts on small entities than the Proposed Alternative, without incrementally contributing to the survival or recovery of *H. hippopus, H. porcellanus, T. derasa, T. gigas T. mbalavuana,* or *T. squamosina*.

Executive Order 12866 and Paperwork Reduction Act

This rulemaking is exempt from review under Executive Order 12866. This proposed rule does not contain a collection-of-information requirement for the purposes of the Paperwork Reduction Act.

Executive Order 13132, Federalism

In accordance with E.O. 13132, we determined that this proposed rule does not have significant federalism effects and that a federalism assessment is not required. In keeping with the intent of the Administration and Congress to provide continuing and meaningful dialogue on issues of mutual State and Federal interest, this proposed rule will be given to the relevant governmental

agencies in the countries in which the species occurs, and they will be invited to comment. As we proceed, we intend to continue engaging in informal and formal contacts with the States, and other affected local, regional, or foreign entities, giving careful consideration to all written and oral comments received.

List of Subjects in 50 CFR Part 223 and 224

Endangered and threatened species.

Dated: July 2, 2024.

Samuel D. Rauch, III,

Deputy Assistant Administrator for Regulatory Programs, National Marine Fisheries Service.

For the reasons set out in the preamble, NMFS proposes to amend 50 CFR parts 223 and 224 as follows:

PART 223—THREATENED MARINE AND ANADROMOUS SPECIES

■ 1. The authority citation for part 223 continues to read as follows:

Authority: 16 U.S.C. 1531 1543; subpart B, § 223.201–202 also issued under 16 U.S.C. 1361 *et seq.*; 16 U.S.C. 5503(d) for § 223.206(d)(9).

■ 2. In § 223.102, amend the table in paragraph (e) by adding new entries for ''Clam, horse's hoof'', ''Giant clam, boring'', ''Giant clam, fluted'', ''Giant clam, Noah's'', and ''Giant clam, small'' in alphabetical order under ''Molluscs'' to read as follows:

§ 223.102 Enumeration of threatened marine and anadromous species.

* * * * * (e) * * *

Species 1 Common Scientific Description Citation(s) for listing determination(s) Critical ESA rules name **Scientific** name Description of listed entity ******* **Molluscs** ******* Clam, horse's hoof *Hippopus hippopus* Entire species *[Federal Register page where the document begins], [date of publication of final rule]*. NA NA Giant clam, boring *Tridacna crocea* Entire species *[Federal Register page where the document begins], [date of publication of final rule]*. NA NA Giant clam, fluted *Tridacna squamosa* Entire species *[Federal Register page where the document begins], [date of publication of final rule]*. NA NA Giant clam, Noah's *Tridacna noae* Entire species *[Federal Register page where the document begins], [date of publication of final rule]*. NA NA Giant clam, small *Tridacna maxima* ... Entire species *[Federal Register page where the document begins], [date of publication of final rule]*. NA NA * * * * * * * * * * * * * * *

1Species includes taxonomic species, subspecies, distinct population segments (DPSs) (for a policy statement, see 61 FR 4722, February 7, 1996), and evolutionarily significant units (ESUs) (for a policy statement, see 56 FR 58612, November 20, 1991).

■ 3. Add § 223.217 to subpart B to read as follows:

§ 223.217 Horse's hoof clam.

Prohibitions. The prohibitions of section $9(a)(1)(A)$ through $9(a)(1)(G)$ of the ESA (16 U.S.C. 1538) relating to endangered species shall apply to the horse's hoof clam (*Hippopus hippopus*) listed in § 223.102.

■ 4. Add § 223.218 to subpart B 223 to read as follows:

§ 223.218 Boring giant clam, small giant clam, Noah's giant clam, fluted giant clam.

(a) *Prohibitions.* It is unlawful for any person subject to the jurisdiction of the United States to import into or export from the United States or its territories any derivative parts or products of the boring giant clam (*Tridacna crocea*), fluted giant clam (*Tridacna squamosa*), Noah's giant clam (*Tridacna noae*), and small giant clam (*Tridacna maxima*) listed in § 223.102. The term ''derivative parts or products'' is defined in this part as:

(1) Any tissue part that has been removed from the shell, including mantle tissue, adductor muscle, portions thereof, or the whole flesh of the animal comprising both the mantle and adductor muscle;

(2) Any worked shell product, including handicrafts, sculptures, jewelry, tableware, decorative ornaments, and other carvings, but not raw, uncarved shells; or

(3) Pearls or any product derived from a pearl.

(b) [Reserved]

PART 224—ENDANGERED MARINE AND ANADROMOUS SPECIES

■ 5. The authority citation for part 224 continues to read as follows:

Authority: 16 U.S.C. 1531–1543 and 16 U.S.C. 1361 *et seq.*

 \blacksquare 6. In § 224.101, amend the table in paragraph (h) by adding new entries for ''Clam, China'', ''Clam, devil'', ''Giant clam, Red Sea'', ''Giant clam, smooth'', and ''Giant clam, true'' in alphabetical

order under Molluscs'' to read as follows:

§ 224.101 Enumeration of endangered marine and anadromous species.

* * * * * (h) * * *

* * * * * * * * * * * * * 1Species includes taxonomic species, subspecies, distinct population segments (DPSs) (for a policy statement, see 61 FR 4722, February 7, 1996), and evolutionarily significant units (ESUs) (for a policy statement, see 56 FR 58612, November 20, 1991).

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